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Helminth and protozoan parasites of subterranean rodents (Chordata, Mammalia, Rodentia) of the world

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Abstract

Published studies and ten new unpublished records included herein reveal that approximately 174 species of endoparasites (helminths and protozoans) are known from 65 of 163 species of rodents that occupy the subterranean ecotope globally. Of those, 94 endoparasite species were originally described from these rodents. A total of 282 host-parasite associations are summarized from four major zoogeographic regions including Ethiopian, Palearctic/Oriental, Nearctic, and Neotropical. Thirty-four parasite records from the literature have been identified to only the level of the genus. In this summary, ten new records have been added, and the most current taxonomic status of each parasite species is noted. Interestingly, there are no data on endoparasites from more than 68% of described subterranean rodents, which indicates that discovery and documentation are at an early stage and must continue.

Keywords

Bathyergidae, Cricetidae, Ctenomyidae, Endoparasite, Geomyidae, Heterocephalidae, Octodontidae, Spalacidae

Introduction

Subterranean rodents are animals adapted to live underground with minimal dependency on surface resources. They exhibit numerous adaptations to maintain their life activities in this niche including almost no externally visible neck, small eyes and ears,

short legs, and very loose skin with soft fur that enables them to turn in their burrows with ease (Maser et al. 1981; Lacey et al. 2000). Conditions within the burrow systems are characterized by complete darkness, constant temperatures, relative humidity of 100% with low levels of air circulation, elevated carbon dioxide levels, and usually closed tunnels.

In contrast to mammals that live on the surface of the soil, subterranean rodents are completely acclimated to live in complex burrow systems below the surface. These animals have the capability to dig burrow systems through many types of friable soils (Lessa et al. 2008). The underground habitat has been invaded by rodents utilizing specialized digging methods in all zoogeographic regions of the world. However, rodents with the ability to dig tunnels underground by utilizing strong digging limbs as well as other morphological and physiological traits occur in all zoogeographic regions except Australia and Antarctica and adaptations by non-phylogenetically related groups to a subterranean existence are considered a product of convergent evolution (Losos 2011). Approximately 40% of the 6,500 mammal species of the world are rodents. Even though only 6.5% of all rodent species occupy the subterranean ecotope, these mammals play an essential part of the ecology in the areas in which they live, functioning as biological plows, cycling the earth, changing the landscape, promoting plant growth and ecological succession, and playing a critical role in cycling carbon and other nutrients through the soil. In the order Rodentia, a total of 163 extant subterranean species across 23 genera, within seven families, has been recognized with distributions throughout all continents except Antarctica and Australia (see Table 1) (Van Daele et al. 2007; Wilson et al. 2016, 2017).

Based on macroevolutionary patterns derived from the study of the fossil record, subterranean rodent species diversity has appeared to have oscillated since early Oligocene time [ca. 36 million years ago, (mya)]. The Geomyidae Bonaparte, 1845 and the Bathyergidae Waterhouse, 1841 have the greatest diversity among all subterranean rodent families relative to the number of genera found throughout evolutionary time and identified thus far as fossil taxa (Cook et al. 2000). Fluctuation cycles in diversification, known as taxon pulses (Erwin 1985) appear to have been driven by local, regional, and global climate oscillations, and explained by the Stockholm Paradigm, which seeks to provide an understanding of the evolution of host-parasite/pathogen systems via the evolutionary process of species diversification following mass extinctions (Brooks et al. 2019).

Ethiopian subterranean rodents

Subterranean rodents in the Ethiopian zoogeographic region are represented by twenty species in seven genera across three families (Heterocephalidae, Bathyergidae, and Spalacidae) including *Heterocephalus* Rüppell, 1842, *Heliophobius* Peters, 1846, *Bathyergus* Illiger, 1811, *Georychus* Illiger, 1811, *Cryptomys* Gray, 1864, *Fukomys* Kock et al., 2006, and *Tachyoryctes* Rüppell, 1835 (see Landry 1957; Patterson and Upham 2014; Wilson et al. 2016).

Table 1. List of subterranean rodents. NA = Nearctic, Nt = Neotropical, E = Ethiopian, P = Palearctic, O = Oriental.

Suborder	Infraorder	Family	Subfamily	Tribe	#	Genus/Species	Region	
Castorimorpha	Geomorpha	Geomyidae	Geomyinae	Thomomyini	1	*Thomomys atrovarius* J. A. Allen, 1898	NA	NA
					2	*Thomomys bottae* (Eydoux & Gervais, 1836)	NA	NA
					3	*Thomomys bulbivorus* (Richardson, 1829)	NA	NA
					4	*Thomomys clusius* Coues, 1875	NA	NA
					5	*Thomomys idahoensis* Merriam, 1901	NA	NA
					6	*Thomomys mazama* Merriam, 1897	NA	NA
					7	*Thomomys monticola* J. A. Allen, 1893	NA	NA
					8	*Thomomys nayarensis* Mathis et al., 2013	NA	NA
					9	*Thomomys sheldoni* Bailey, 1915	NA	NA
					10	*Thomomys talpoides* (Richardson, 1828)	NA	NA
					11	*Thomomys townsendii* (Bachman, 1839)	NA	NA
					12	*Thomomys umbrinus* (Richardson, 1829)	NA	NA
				Geomyini	13	*Geomys arenarius* Merriam, 1895	NA	NA
					14	*Geomys attwateri* Merriam, 1895	NA	NA
					15	*Geomys breviceps* Baird, 1855	NA	NA
					16	*Geomys bursarius* (Shaw, 1800)	NA	NA
					17	*Geomys jugossicularis* Hooper, 1940	NA	NA
					18	*Geomys knoxjonesi* Baker & Genoways, 1975	NA	NA
					19	*Geomys lutescens* Merriam, 1890	NA	NA
					20	*Geomys personatus* True, 1889	NA	NA
					21	*Geomys pinetis* Rafinesque, 1817	Nt	Nt
					22	*Geomys streckeri* Davis, 1943	NA	NA
					23	*Geomys texensis* Merriam, 1895	NA	NA
					24	*Geomys tropicalis* Goldman, 1915	NA	NA
					25	*Zygogeomys trichopus* Merriam, 1895	Nt	Nt
					26	*Orthogeomys grandis* (Thomas, 1893)	NA	Nt
Castorimorpha	Geomorpha	Geomyidae	Geomyinae	Geomyini	27	*Heterogeomys cavator* (Bangs, 1902)	Nt	Nt
					28	*Heterogeomys cherriei* (J. A. Allen, 1893)	Nt	Nt
					29	*Heterogeomys dariensis* (Goldman, 1912)	Nt	Nt
					30	*Heterogeomys heterodus* (Peters, 1865)	Nt	Nt
					31	*Heterogeomys hispidus* (Le Conte, 1852)	Nt	Nt
					32	*Heterogeomys lanius* Elliot, 1905	Nt	Nt
					33	*Heterogeomys underwoodi* Osgood, 1931	Nt	Nt
					34	*Pappogeomys bulleri* (Thomas, 1892)	Nt	Nt
					35	*Cratogeomys castanops* (Baird, 1852)	NA	Nt
					36	*Cratogeomys fulvescens* Merriam, 1895	NA	Nt
					37	*Cratogeomys fumosus* (Merriam, 1892)	Nt	Nt
					38	*Cratogeomys goldmani* (Merriam, 1895)	NA	Nt
					39	*Cratogeomys merriami* (Thomas, 1893)	Nt	Nt
					40	*Cratogeomys perotensis* Merriam, 1895	NA	Nt
					41	*Cratogeomys planiceps* (Merriam, 1895)	NA	Nt
Hystricomorpha	Histricognathi	Ctenomyidae			42	*Ctenomys andersoni* Gardner et al., 2014	Nt	Nt
					43	*Ctenomys argentinus* J. R. Contreras & Berry, 1982	Nt	Nt
					44	*Ctenomys australis* Rusconi, 1934	Nt	Nt
					45	*Ctenomys azarae* Thomas, 1903	Nt	Nt
					46	*Ctenomys bergi* Thomas, 1902	Nt	Nt
					47	*Ctenomys bicolor* Miranda-Ribeiro, 1914	Nt	Nt
					48	*Ctenomys boliviensis* Waterhouse, 1848	Nt	Nt
					49	*Ctenomys bonettoi* J. R. Contreras & Berry, 1982	Nt	Nt
					50	*Ctenomys brasiliensis* de Blainville, 1826	Nt	Nt
					51	*Ctenomys colburni* J. A. Allen, 1903	Nt	Nt
					52	*Ctenomys coludo* Thomas, 1920	Nt	Nt
					52	*Ctenomys coludo* Thomas, 1920	Nt	Nt
					53	*Ctenomys conoveri* Osgood, 1946	Nt	Nt

Suborder	Infraorder	Family	Subfamily	Tribe	#	Genus/Species	Region	
Hystricomorpha	Histricognathi	Ctenomyidae			54	*Ctenomys coyhaiquensis* Kelt & Gallardo, 1994	Nt	Nt
					55	*Ctenomys dorbignyi* Contreras & Contreras, 1984	Nt	Nt
					56	*Ctenomys dorsalis* Thomas, 1900	Nt	Nt
					57	*Ctenomys emilianus* Thomas & S. Leger, 1926	Nt	Nt
					58	*Ctenomys erikacuellarae* Gardner et al., 2014	Nt	Nt
					59	*Ctenomys famosus* Thomas, 1920	Nt	Nt
					60	*Ctenomys flamarioni* Travi, 1981	Nt	Nt
					61	*Ctenomys fodax* Thomas, 1910	Nt	Nt
					62	*Ctenomys fochi* Thomas, 1919	Nt	Nt
					63	*Ctenomys frater* Thomas, 1902	Nt	Nt
					64	*Ctenomys fulvus* Philippi, 1860	Nt	Nt
					65	*Ctenomys goodfellowi* Thomas, 1921	Nt	Nt
					66	*Ctenomys haigi* Thomas, 1919	Nt	Nt
					67	*Ctenomys ibicuiensis* Freitas et al., 2012	Nt	Nt
					68	*Ctenomys johannis* Thomas, 1921	Nt	Nt
					69	*Ctenomys juris* Thomas, 1920	Nt	Nt
					70	*Ctenomys knighti* Thomas, 1919	Nt	Nt
					71	*Ctenomys lami* Freitas, 2001	Nt	Nt
					72	*Ctenomys latro* Thomas, 1918	Nt	Nt
					73	*Ctenomys lessai* Gardner et al., 2014	Nt	Nt
					74	*Ctenomys leucodon* Waterhouse, 1848	Nt	Nt
					75	*Ctenomys lewisi* Thomas, 1926	Nt	Nt
					76	*Ctenomys magellanicus* Bennett, 1836	Nt	Nt
					77	*Ctenomys mariafarelli* Azurduy, 2005	Nt	Nt
					78	*Ctenomys maulinus* Philippi, 1872	Nt	Nt
					79	*Ctenomys mendocinus* Philippi, 1869	Nt	Nt
					80	*Ctenomys minitus* Nehring, 1887	Nt	Nt
					81	*Ctenomys nattereri* Wagner, 1848	Nt	Nt
					82	*Ctenomys occultus* Thomas, 1920	Nt	Nt
					83	*Ctenomys opimus* Wagner, 1848	Nt	Nt
					84	*Ctenomys osvaldoreigi* J. R. Contreras, 1985	Nt	Nt
					85	*Ctenomys paraguayensis* J. R. Contreras, 2000	Nt	Nt
					86	*Ctenomys pearsoni* Lessa & Langguth, 1983	Nt	Nt
					87	*Ctenomys perrensi* Thomas, 1896	Nt	Nt
					88	*Ctenomys peruanus* Sanborn & Pearson, 1947	Nt	Nt
					89	*Ctenomys pilarensis* J. R. Contreras, 1993	Nt	Nt
					90	*Ctenomys pontifex* Thomas, 1918	Nt	Nt
					91	*Ctenomys porteousi* Thomas, 1916	Nt	Nt
					92	*Ctenomys pundti* Nehring, 1900	Nt	Nt
					93	*Ctenomys rionegrensis* Langguth & Abella, 1970	Nt	Nt
					94	*Ctenomys roigi* J. R. Contreras, 1988	Nt	Nt
					95	*Ctenomys rondoni* Miranda-Ribeiro, 1914	Nt	Nt
					96	*Ctenomys rosendopascuali* J. R. Contreras, 1995	Nt	Nt
					97	*Ctenomys talarum* Thomas, 1898	Nt	Nt
					98	*Ctenomys torquatus* Lichtenstein, 1830	Nt	Nt
					99	*Ctenomys tuconax* Thomas, 1925	Nt	Nt
					100	*Ctenomys tucumanus* Thomas, 1900	Nt	Nt
					101	*Ctenomys tulduco* Thomas, 1921	Nt	Nt
					102	*Ctenomys saltarius* Thomas, 1912	Nt	Nt
					103	*Ctenomys scagliai* J. R. Contreras, 1999	Nt	Nt
					104	*Ctenomys sericeus* J. A. Allen, 1903	Nt	Nt
					105	*Ctenomys sociabilis* Pearson & Christie, 1985	Nt	Nt
					106	*Ctenomys steinbachi* Thomas, 1907	Nt	Nt
					107	*Ctenomys validus* J. R. Contreras et al., 1977	Nt	Nt
					108	*Ctenomys viperinus* Thomas, 1926	Nt	Nt
					109	*Ctenomys yatesi* Gardner et al., 2014	Nt	Nt
					110	*Ctenomys yolandae* J. R. Contreras & Berry, 1984	Nt	Nt

Suborder	Infraorder	Family	Subfamily	Tribe	#	Genus/Species	Region	
Hystricomorpha	Histricognathi	Octodontidae			111	*Spalacopus cyanus* (Molina, 1782)	Nt	Nt
		Hetero-cephalidae			112	*Heterocephalus glaber* Rüppell, 1842	E	E
		Bathyergidae			113	*Heliophobius argenteocinereus* Peters, 1846	E	E
					114	*Bathyergus janetta* Thomas & Schwann, 1904	E	E
					115	*Bathyergus suillus* (Schreber, 1782)	E	E
					116	*Georychus capensis* (Pallas, 1778)	E	E
					117	*Cryptomys hottentotus* (Lesson, 1826)	E	E
					118	*Fukomys amatus* (Wroughton, 1907)	E	E
					119	*Fukomys anselli* (Burda et al., 1999)	E	E
					120	*Fukomys bocagei* (de Winton, 1897)	E	E
					121	*Fukomys damarensis* (Ogilby, 1838)	E	E
					122	*Fukomys darlingi* (Thomas 1895)	E	E
					123	*Fukomys foxi* (Thomas, 1911)	E	E
					124	*Fukomys kafuensis* (Burda et al., 1999)	E	E
					125	*Fukomys mechowii* (Peters, 1881)	E	E
					126	*Fukomys ochraceocinereus* (Heuglin, 1846)	E	E
					127	*Fukomys vandewoestijneae* Van Daele et al., 2013	E	E
					128	*Fukomys whytei* (Thomas, 1897)	E	E
					129	*Fukomys zechi* (Matschie, 1900)	E	E
Myomorpha		Cricetidae	Arvicolinae	Prometheo-myini	130	*Prometheomys schaposchnikowi* Satunin, 1901	P	P
				Ellobiusini	131	*Ellobius alaicus* Vorontsov et al., 1969	P	P
					132	*Ellobius fuscocapillus* (Blyth, 1843)	P	P
					133	*Ellobius lutescens* Thomas, 1897	P	P
					134	*Ellobius talpinus* (Pallas, 1770)	P	P
					135	*Ellobius tancrei* Blasius, 1884	P	P
		Spalacidae	Myospalaci-nae		136	*Myospalax armandii* (Milne-Edwards, 1867)	P	P
					137	*Myospalax aspalax* (Pallas, 1776)	P	P
					138	*Myospalax epsilanus* Thomas, 1912	P	P
					139	*Myospalax myospalax* (Laxmann, 1773)	P	P
					140	*Myospalax psilurus* (Milne-Edwards, 1874)	P	P
					141	*Eospalax baileyi* (Thomas, 1911)	P	P
					142	*Eospalax cansus* (Lyon, 1907)	P	P
					143	*Eospalax fontanierii* (Milne-Edwards, 1867)	P	P
					144	*Eospalax rothschildi* (Thomas, 1911)	P	P
					145	*Eospalax rufescens* (J. A. Allen, 1909)	P	P
					146	*Eospalax smithii* (Thomas, 1911)	P	P
			Rhizomyi-nae	Rhizomyini	147	*Rhizomys pruinosus* (Blyth, 1851)	P	O
					148	*Rhizomys sinensis* Gray, 1831	P	O
					149	*Rhizomys sumatrensis* (Raffles, 1821)	O	O
					150	*Cannomys bodius* (Hodgson, 1841)	O	O
				Tachyor-yctini	151	*Tachyoryctes macrocephalus* (Rüppell, 1842)	E	E
					152	*Tachyoryctes splendens* (Rüppell, 1835)	E	E
			Spalacinae		153	*Spalax antiquus* Méhely, 1909	P	P
					154	*Spalax arenarius* Reshetnik, 1939	P	P
					155	*Spalax giganteus* Nehring, 1898	P	P
					156	*Spalax graecus* Nehring, 1898	P	P
					157	*Spalax istricus* Méhely, 1909	P	P
					158	*Spalax microphthalmus* Güldenstädt, 1770	P	P
					159	*Spalax uralensis* Tiflov & Usov, 1939	P	P
					160	*Spalax zemni* (Erxleben, 1777)	P	P
					161	*Nannospalax ehrenbergi* Nehring, 1898	P	P
					162	*Nannospalax leucodon* (Nordmann, 1840)	P	P
					163	*Nannospalax xanthodon* (Nordmann, 1840)	P	P

Nearctic subterranean rodents

Species of the family Geomyidae are endemic to the Nearctic and northern Neotropics and are known collectively as pocket gophers due to presence of fur-lined cheek pouches in all species. They are a monophyletic group of subterranean rodents that share common ancestry with rodents of the family Heteromyidae (Wilson et al. 2016). Pocket gophers inhabit a wide geographic range, extending from a northernmost limit in southwest and south-central Canada through the central and western United States, southeast into central Florida, and south into Mexico and through Central America into Panama and near the Rio Atrato in northern Colombia (Hall 1981; Alberico 1990; Solari et al. 2013). As in most subterranean rodents, pocket gophers are fusiform in shape, having a naked and sensitive tail (they can run backwards as fast as they can forwards, using their tail as a rear-guide sensor (Gardner, pers. obs.). They have small pinnae, loose skin, and their fur-lined cheek pouches are used only for food transport (Howard and Childs 1959; Maser et al. 1981; Hafner 1982; Honeycutt and Williams 1982; Hafner et al. 1994). The family consists of seven extant genera and 41 species (Wilson et al. 2016). The genus *Thomomys* Wied-Niewied, 1839, has 12 species and many subspecies, making this genus the most speciose of the family Geomyidae (see Patton 2005).

Palearctic subterranean rodents

Thirty-two species of subterranean rodents of seven genera in two families, including Cricetidae Fischer, 1817, and Spalacidae Gray, 1821, occur in the Palearctic region. Those include *Prometheomys* Satunin, 1901, and *Ellobius* Fischer, 1814, in the family Cricetidae, which includes the subfamily Arvicolinae Gray, 1821. The genera *Myospalax* Laxmann, 1769, *Eospalax* Allen, 1938, *Rhizomys* Gray, 1831, *Cannomys* Thomas, 1915, *Spalax* Guldenstaedt, 1770, and *Nannospalax* (Nordmann, 1840) are in the family Spalacidae which includes the subfamilies Myospalacinae Lilljeborg, 1866, Rhizomyinae Winge, 1887, and Spalacinae Gray, 1821. Among all subterranean forms of the Rodentia, those occurring in the Palearctic region have the most extensive geographic distribution. Based on fossil evidence, the first known subterranean species of rodents appeared in the early Pliocene of Asia (Repenning 1984; Repenning et al. 1990). *Rhizomys pruinosus* (Blyth, 1851) and *Rhizomys sinensis* Gray, 1831 occur in the Palearctic and Oriental zoogeographic regions. At the current time, only two species of subterranean rodents are known from the Oriental region, and those include *Rhizomys sumatrensis* (Raffles, 1821) and *Cannomys bodius* (Hodgson, 1841).

Neotropical subterranean rodents

The Neotropical subterranean rodents are represented by two hystricognath Caviomorph families, the Ctenomyidae Lesson, 1842 and Octodontidae Waterhouse, 1839. The family Ctenomyidae currently includes only species in the genus *Ctenomys* Blainville, 1826 which are known as the tuco-tucos, with approximately 69 described

species. These rodents occur in suitable habitats with a geographic distribution from southern Peru and southwestern Brazil south to Tierra de Fuego through Chile, Argentina, Bolivia, Paraguay, and Uruguay (Reig et al. 1990; Gardner et al. 2014). The fossil record indicates that species that can be allocated to the family Ctenomyidae originated ca. 10 mya (Cook et al. 2000), with rapid diversification in the genus *Ctenomys* commencing at ca. 3 mya (Parada et al. 2011). Interestingly, the single subterranean species in the Octodontidae which are the sister taxon of the Ctenomyidae includes the monotypic *Spalacopus cyanus* (Molina, 1782) and these occur only in central Chile.

Endoparasites

Our analysis shows that endoparasites have been found and reported from fewer than 40% of known species of subterranean rodents world-wide. There are several factors that could potentially explain this lack of reported data as researchers face several challenges when trapping subterranean rodents; without prior training, just finding and then determining active subterranean mammal burrow mounds is difficult. There could be thousands of burrow mounds, but researchers need acute field expertise to identify freshly dug burrows to capture these animals. Moreover, setting subterranean rodent traps is labor intensive and time-consuming, demanding lots of patience, physical strength, and luck.

Another problem is that sampling of species of subterranean rodents has not been systematically carried out and most collecting was done over time that was rather scattered and sporadic, and very few collections included parasites in their investigations. Many previous studies have failed to record comprehensive data during their collections of mammals and other vertebrates, discarding the internal organs of collected mammals without further examination. This practice resulted in significant gaps in parasite data with black holes regarding their faunas of both ecto- and endoparasites. Parasites discovered in research projects contain vital information about themselves and their host life history, consisting of information that we cannot ignore. The work presented here represents a synthesis of all available literature on the endoparasites of subterranean rodents of the world, as such, some references and works may have been missed, but we hope that this list provides a starting point for other researchers interested in this area of study.

Materials and methods

The current checklist was created by accumulating all published references arranged in a chronologically ordered tabular form representing globally each continent. The taxonomic status of each host and parasite species are up to date and represent the most current classifications. Most of the early literature was located in the reprint library of the H.W. Manter Laboratory of Parasitology in the University of Nebraska State Museum. Some of the literature was obtained from the Digital Commons at

University of Nebraska-Lincoln Libraries while several rare international references were obtained through interlibrary loan. For new records presented herein, some samples were collected during the field Parasitology class in western Nebraska and others were included from field work by S.L. Gardner in the 1980's the 1990's and earlier. Except for a few instances that we detail in the results, we used the original taxonomic names of both the hosts and parasites as published in the original literature. Throughout this paper, we used the zoogeographic terminology first established by Wallace (1876) (Rueda et al. 2013).

Results

Literature review

Ethiopian subterranean rodent endoparasites

See graphical summary in Fig. 1 and endoparasite diversity list in Table 2.

Diesing (1864) reported the first helminth parasite species from a subterranean rodent host, where *Taenia spalacis* (Diesing, 1864) was reported from *Georychus capensis* (Pallas, 1779) collected from Port Natal, South Africa.

Ortlepp (1939) described three new nematode species from the Cape dune mole-rat, *Bathyergus suillus* (Schreber, 1782) (Bathyergidae: Rodentia) collected from Strandfontein and Cape Town, South Africa including: *Libyostrongylus bathyergi* Ortlepp, 1939, *Longistriata bathyergi*, and *Mammalakis macrospiculum* (see Ortlepp 1939; Inglis 1991). These represent the first known reports of parasitic nematodes from African subterranean rodents. Interestingly, all these species have been reclassified into different genera and are currently known as *Paralibyostrongylus bathyergi*, *Ortleppstrongylus bathyergi*, and *Mammalakis macrospiculum*, (see De Graaff 1964; Lutermann and Bennett 2012).

Fain (1956) reported *Taenia brauni* Setti, 1897, from *Tachyoryctes splendens* (Rüppell, 1835) collected in Ruanda-Urundi, East Africa. After a period of several years, De Graaff (1964) mentioned that in a personal communication that he had with Ortlepp an unidentified tapeworm was obtained by Ortlepp from *Bathyergus suillus*, collected at Houtbay, near Cape Town. Also, De Graaff (1964) wrote that Ortlepp told him that he found cysts of an unidentified species of *Echinococcus* Rudolphi, 1801 obtained from the muscles of the abdominal cavity as well as liver of *G. capensis* collected at Wynberg, near Cape Town, South Africa (Hüttner and Romig 2009).

Levine and Ivens (1965) described the first coccidian parasite, *Eimeria heterocephali* from the mucosal epithelial cells of the cecum of a *Heterocephalus glaber* specimen collected at Somaliland or Kenya, South Africa.

Schmidt and Canaris (1968) reported *Ascarops africana* (Sandground, 1933) from *Tachyoryctes macrocephalus* (Rüppell, 1842) collected from Njoro, Kenya, East Africa.

Several years later, De Graaff (1981) reported *Inermicapsifer madagascariensis* (Davaine, 1870) from the Common mole-rat, *Cryptomys hottentotus* (Lesson, 1826) (Bathyergidae: Hystricomorpha), collected from Shingwedzi, South Africa.

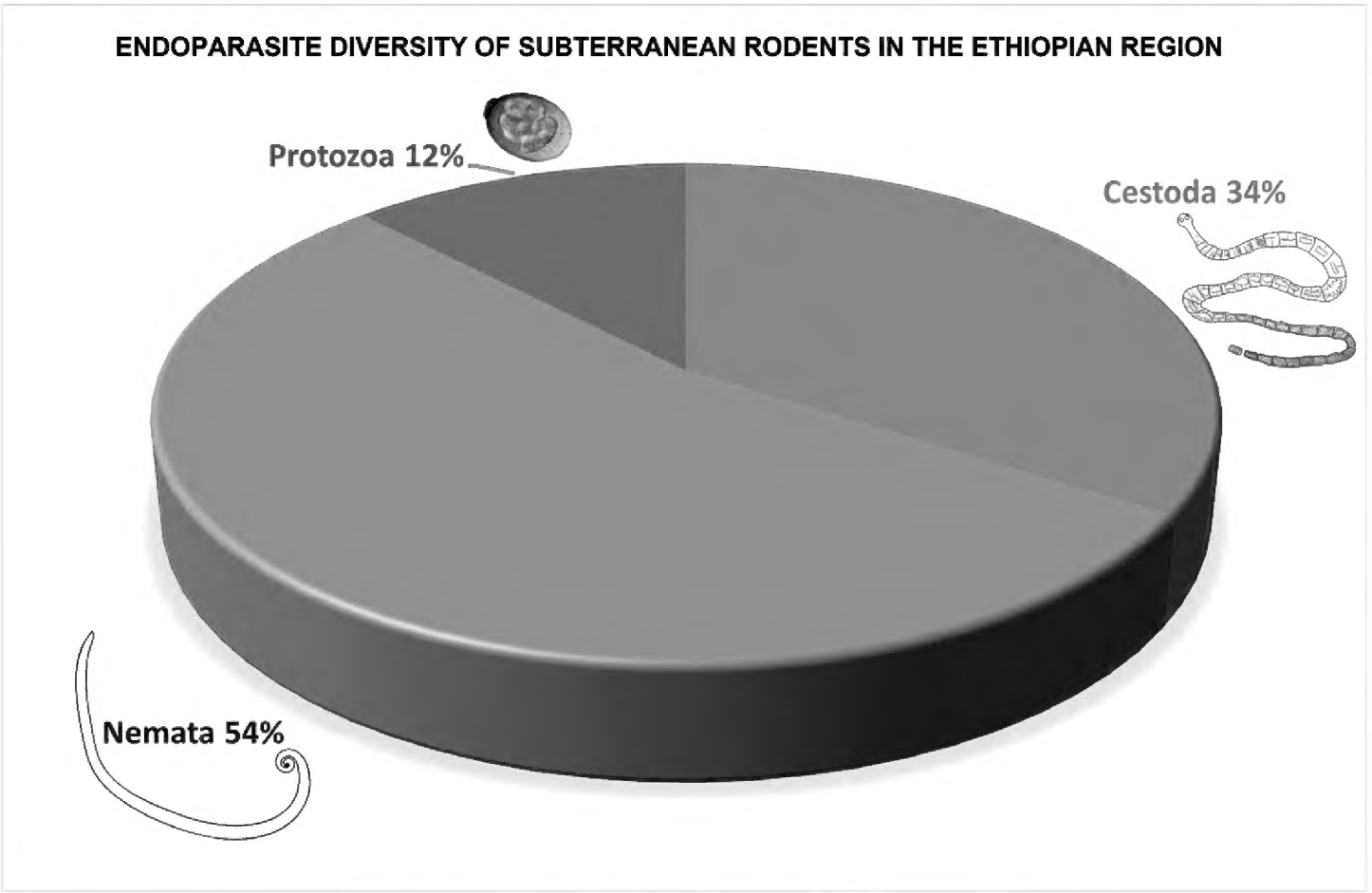

Figure 1. Pie diagram representing percentage taxon composition of the higher classification of endoparasite diversity found infecting subterranean rodents from the Ethiopian zoogeographic region derived from records in the literature published from 1864 through 2018. The Nemata are the most speciose representing 54% of the total endoparasite fauna, followed by Cestoda (34%), and Protozoa (12%).

Scharff et al. (1997) reported *Inermicapsifer madagascariensis* from the small intestine, and *Protospirura muricola* (Gedoelst, 1916) from the colon of *Fukomys kafuensis* (Burda et al., 1999) collected from Itezhi-Tezhi, Zambia. They also found an unidentified species of *Calodium* Moravec, 1982 (syn. *Capillaria* Zeder, 1800) (eggs only), *I. madagascariensis*, and an unknown *Raillietina* Fuhrman, 1920, from the small intestine, and *P. muricola* from the abdominal cavity of *Fukomys mechowii* (Peters, 1881) collected from Ndole, Zambia. The discovery of *P. muricola* in the abdominal cavity was probably a result of these nematodes moving from the stomach during or after the necropsy event of the individual *F. mechowii* mentioned.

Koudela et al. (2000) described *Eimeria burdai*, as a new species of coccidian from the subterranean African silvery mole-rat, *Heliophobius argenteocinereus* Peters, 1846, collected from Lubalashi Province, central Zambia.

Baruš et al. (2003) studied the relative concentration of heavy metals in helminth parasites; several Silvery mole-rats, *H. argenteocinereus*, were necropsied for their internal parasite tissues collected from the Blantyre-Limbe region of Malawi, southeastern Africa. As a result, two species of helminths were found, including *Inermicapsifer arvicanthidis* (Kofend, 1917) and *Protospirura muricola*, and these specimens were later examined for four heavy metal elements (cadmium, copper, lead, and zinc), and compared against the liver and muscle tissues of their hosts. The same species of parasites from these same hosts were reported by Tenora et al. (2003).

Table 2. Endoparasite species diversity of Ethiopian subterranean rodents and their known original hosts. Authorities are given for parasite and host species.

Host species	Parasite species	References
Bathyergus suillus (Schreber, 1782)	*Mammalakis macrospiculum* (Ortlepp, 1939)	Lutermann et al. 2012
	Ortleppstrongylus bathyergi Ortlepp, 1939	De Graaff 1964
	Paralibyostrongylus bathyergi (Ortlepp, 1939)	Lutermann et al. 2012
	Rodentolepis Spasskii, 1954	Lutermann et al. 2012
	Taenia Linnaeus, 1758	Lutermann et al. 2012
	Trichostrongylus Looss, 1905	De Graaff 1964
	Trichuris Roederer, 1761	Lutermann et al. 2012
Cryptomys hottentotus (Lesson, 1826)	*Ascarops africana* (Sandground, 1933)	Lutermann et al. 2013
	Heligmonina Baylis, 1928	Viljoen et al. 2011
	Inermicapsifer madagascariensis (Davaine, 1870)	De Graaff 1981
	Mammalakis macrospiculum (Ortlepp, 1939)	Archer et al. 2017
	Mathevotaenia Akhumyan, 1946	Viljoen et al. 2011
	Neoheligmonella Durette-Desset, 1971	Archer et al. 2017
	Protospirura Seurat, 1914	Viljoen et al. 2011
	Raillietina Fuhrman, 1920	Lutermann et al. 2013
	Trichuris Roederer, 1761	Archer et al. 2017
Fukomys anselli (Burda et al., 1999)	*Hexametra* Travassos, 1920	Lutermann et al. 2018
	Inermicapsifer Janicki, 1910	Lutermann et al. 2018
	Mammalakis zambiensis Junker et al., 2017	Junker et al. 2017
	Protospirura muricola (Gedoelst, 1916)	Lutermann et al. 2018
	Protospirura numidica Seurat, 1914	Lutermann et al. 2018
	Protospirura Seurat, 1914	Lutermann et al. 2018
	Rodentolepis cf. *microstoma* (Dujardin, 1945)	Lutermann et al. 2018
Fukomys kafuensis (Burda et al., 1999)	*Inermicapsifer madagascariensis* (Davaine, 1870)	Scharff et al. 1997
	Protospirura muricola (Gedoelst, 1916)	Scharff et al. 1997
Fukomys mechowii (Peters, 1881)	*Capillaria* Zeder, 1800	Scharff et al. 1997
	Inermicapsifer madagascariensis (Davaine, 1870)	Scharff et al. 1997
	Protospirura muricola (Gedoelst, 1916)	Scharff et al. 1997
	Raillietina Fuhrman, 1920	Scharff et al. 1997
Georychus capensis (Pallas, 1778)	*Coenurus spalacis* Diesing, 1864	Diesing 1864
	Echinococcus Rudolphi, 1801	De Graaff 1964; Hüttner and Romig 2009
	Trichuris Roederer, 1761	Lutermann et al. 2012
Heliophobius argenteocinereus Peters, 1846	*Eimeria burdai* Koudela et al., 2000	Koudela et al. 2000
	Eimeria heliophobii Modrý et al., 2005	Modrý et al. 2005
	Eimeria nafuko Modrý et al., 2005	Modrý et al. 2005
	Eimeria yamikamiae Modrý et al., 2005	Modrý et al. 2005
	Inermicapsifer arvicanthidis (Kofend, 1917)	Baruš et al. 2003; Tenora et al. 2003
	Protospirura muricola (Gedoelst, 1916)	Baruš et al. 2003; Tenora et al. 2003
Heterocephalus glaber Rüppell, 1842	*Eimeria heterocephali* Levine & Ivens, 1965	Levine and Ivens 1965
Tachyoryctes splendens (Rüppell, 1835)	*Taenia brauni* Setti, 1897	Fain 1956
Tachyoryctes macrocephalus (Rüppell, 1842)	*Ascarops africana* (Sandground, 1933)	Schmidt and Canaris 1968

Modrý et al. (2005) described three new species of *Eimeria* from the Silvery mole-rat *H. argenteocinereus* from Malawi, including: *Eimeria heliophobii*, *E. nafuko*, and *E. yamikamiae* extracted from the fecal samples from the host specimens.

Viljoen et al. (2011), in an ecological study of the role of host traits, season, and group size on parasite burdens in a cooperative breeding mammal, captured 87 individual mole-rats were from the Tshwane region of South Africa in different seasons. Three helminths that were not identified to the species level were obtained from

the small intestine of *Cryptomys hottentotus*, including *Heligmonina* sp. Baylis, 1928, *Mathevotaenia* sp. Akhumyan, 1946, and *Protospirura* sp. Seurat, 1914.

Lutermann and Bennett (2012), during a year-long joint research and eradication project for *Bathyergus suillus* at Cape Town International Airport, Cape Town, South Africa, found these rodents infected with three species of nematodes, including: *Mammalakis macrospiculum*, *Paralibyostrongylus bathyergi*, and *Trichuris* sp. Roederer, 1761, and two species of tapeworms, *Rodentolepis* sp. Spasskii, 1954, and *Taenia* sp. Linnaeus, 1758.

Just one year later, Lutermann et al. (2013), during the study on energetic benefits and costs of parasitism in a cooperative mammal identified *Raillietina* sp., and *Ascarops africana* from the small intestine of *Cryptomys hottentotus* collected from KwaZulu-Natal, South Africa.

Archer et al. (2017), in a seasonal comparative study between two Common mole-rat populations found *Mammalakis macrospiculum*, *Neoheligmonella* Durette-Desset, 1971, and *Trichuris* sp. in *Cryptomys hottentotus* collected from two different habitats, including an arid site, 25 km outside of Kamieskroon, the Northern Cape and a mesic site near Darling, western Cape, South Africa.

Junker et al. (2017) described a new species of ascaridid nematode, *Mammalakis zambiensis* acquired from the large intestine and cecum of Ansell's mole-rat, *Fukomys anselli* (Burda et al., 1999), captured from west of Lusaka at Mukulaikwa Farm Block, Zambia.

Lutermann et al. (2018) reported the following gastrointestinal parasites from Ansell's mole-rat, *F. anselli* in Zambia. Those include *Hexametra* sp. Travassos, 1920, *Inermicapsifer* sp. Janicki, 1910, *Protospirura muricola*, *Protospirura numidica* Seurat, 1914, and *Rodentolepis* cf. *microstoma* (Dujardin, 1945).

Palearctic subterranean rodent endoparasites

See graphical summary in Fig. 2 and endoparasite list in Table 3.

Interestingly, even though helminthology began in Europe (the western Palearctic) in the late 1800's with the work of Leuckart, it was not until the 1920's when Schulz (1927) described the first two species of helminth parasites from two species of subterranean rodents from the Palearctic region. First, *Physocephalus ellobii* Schulz, 1927 was found from the stomach of *Ellobius tancrei* Blasius, 1884 collected from Kotlyrevsky, the northern Caucasus region of Russia. Second, *Gongylonema longispiculum spalacis* Schulz, 1927 was described as the first subspecies found under the mucous membrane of the stomach of *Spalax microphthalmus* Güldenstädt, 1770 collected from the village Kurichya Kosa near the Don River region north of the coast of the Sea of Azov, Russia. Soon after, Marcu (1930) described *Mammalakis spalacis* Marcu, 1930 also obtained from *S. microphthalmus* collected from Romania.

Somewhat later, Schulz and Aloyan (1950), described *Ascaris spalacis* Schulz & Aloyan, 1950 from Lesser mole-rat, *Nannospalax leucodon* (Nordmann, 1840). Kirshenblat collected the materials included in the description from near the small towns of

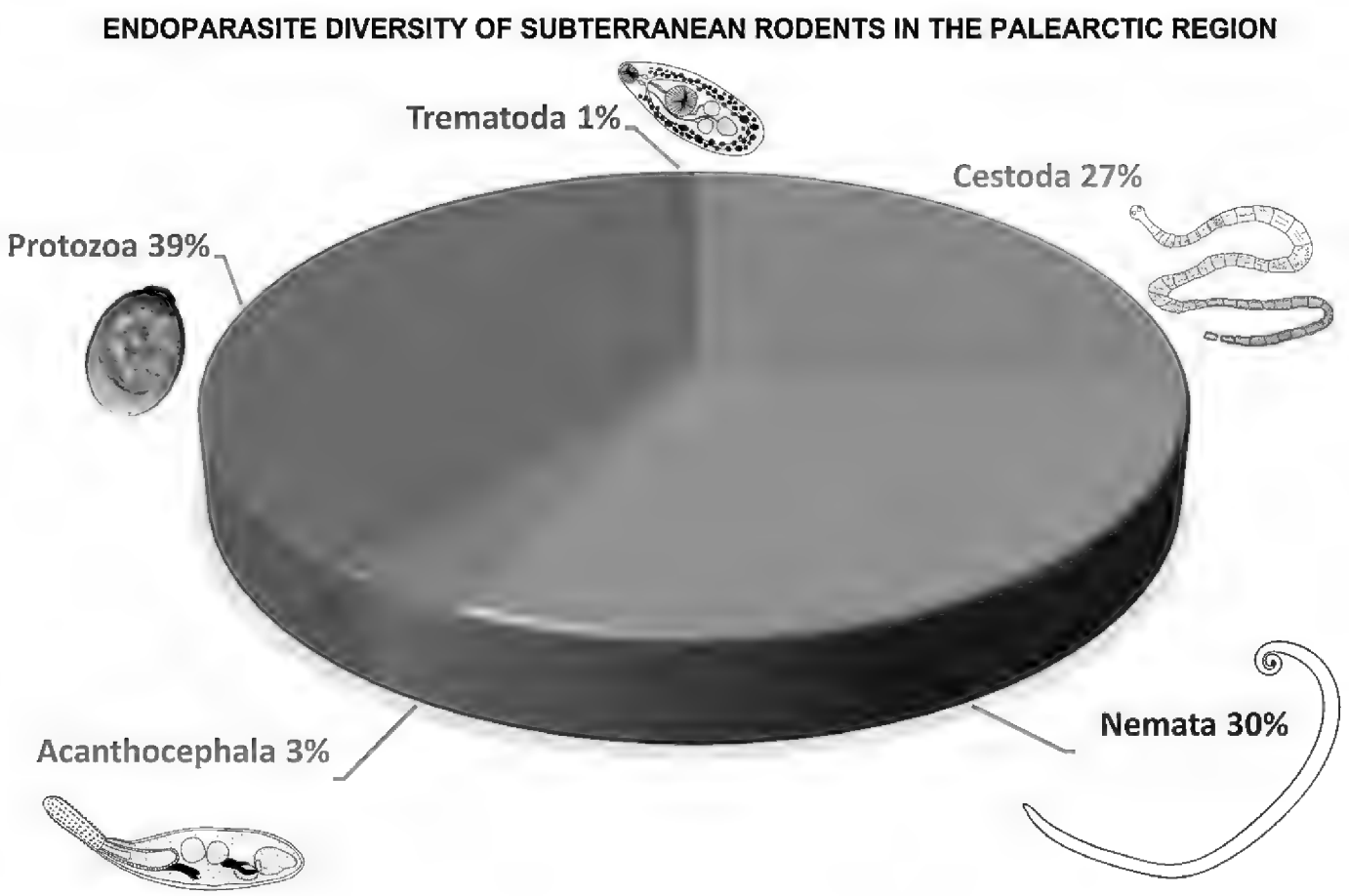

Figure 2. Pie chart showing percentage of infection summary of the higher-level classification of endoparasite diversity among Palearctic subterranean rodents derived from a survey of published records from 1927 through 2022. Protozoa constitute the greatest diversity of endoparasites accounting for 39% of the total parasite species recovered followed by Nemata (30%), Cestoda (27%), Acanthocephala (3%), and the Trematoda coming in at only 1%.

Amamla and Chandura, of the Spitakskii and Akhalkalakskii regions of Armenia, in 1947. All these nematode samples were found from the small intestines of the hosts, necropsied by Aloyan in 1948.

Petrov and Potechina (1953) described *Trichuris spalacis* from *S. microphthalmus* collected from an unspecified locality in Ukraine.

Razumova (1957) reported the following helminth parasites found in specimens of the Long-clawed mole vole, *Prometheomys schaposchnikowi* Satunin, 1901, captured from Ossetia, Russia. These include *Dicrocoelium dendriticum* (Rudolphi, 1819), *Heligmosomum halli* (Schulz, 1926), *Microcephaloides* Haukisalmi et al., 2008, *Taenia polyacantha* Leuckart, 1856, and *Hydatigera* (syn. *Taenia*) *taeniaeformis* (Batsch, 1786).

Tokobaev (1960) reported the collection of *Ellobius talpinus* (Pallas, 1770) from the Kyrgyz Republic and found larvae of *Echinococcus multilocularis* from the liver. In the same report, he reported *Aprostatandrya macrocephala* Douthitt, 1915, from the small intestine and larvae of *Mesocestoides* Vaillant, 1863 from the body cavity, liver, and small intestines. In work on mole voles just a short time later, Zanina and Tokobaev (1962) reported *Catenotaenia pusilla* Goeze, 1782, *Hymenolepis diminuta* Rudolphi,

1819, *Moniliformis moniliformis* Bremser, 1811, and *Hydatigera* (syn. *Taenia*) *taeniaeformis* (Batsch, 1786) from *E. talpinus* collected in Tajikistan.

Andreiko (1963) reported that from 1959 through 1962, 70 Lesser mole-rats, (*Nannospalax leucodon*) collected from the central part of Moldova, Romania had the following helminths: *Mammalakis spalacis* from the cecum, *Taenia straminea* (Goeze, 1782) Spasskii, 1954 and unidentified species of *Aprostatandrya* Kirshenblat, 1938 from the small intestine. In addition, she described *Heligmosomum moldovensis* Andreiko, 1963 from the small intestine of *N. leucodon*.

Kozlov and Yangolenko (1963) described *Ganguleterakis spalaxi* Kozlov & Yangolenko, 1963 from *Spalax microphthalmus* collected from Ukraine.

Kirshenblat (1965) described a new species of nematode *Heligmosomum spalacis* from the small intestine of the mole-rat *Spalax graecus* Nehring, 1898 collected from Chernivtsi, Ukraine.

Levine and Ivens (1965) described two species of *Eimeria* Fischer, 1814 from the Northern mole vole, including: *Ellobius kazakhstanensis* Levine & Ivens, 1965, and *Ellobius talpini* Levine & Ivens, 1965 from the fecal of *Ellobius talpinus* collected from Kazakhstan.

Musaev and Veisov (1963) described *Eimeria lutescenae* Musaev & Veisov, 1963 from *Ellobius lutescens* Thomas, 1897 from Nakhichevanskaia, Azerbaijan. In addition, two *Eimeria* (Schneider, 1875) species were reported with their descriptions, including: *Eimeria ellobii* Svanbaev, 1965 and *Eimeria tadshikistanica* Veisov, 1964 from *Ellobius talpinus* collected from Tajikistan.

Shaykenov and Mahmutov (1968) reported *Echinococcus multilocularis* found in *Myospalax myospalax* (Laxmann, 1773) collected from eastern Kazakhstan. This record is considered a new intermediate host for this tapeworm. Also in the same year, Mészáros (1968) reported the occurrence of *Heligmosomum spalacis* recovered from the Lesser mole-rat, *Nannospalax leucodon*, collected from Hungary.

Murai (1968) recorded the Lesser mole-rat, *N. leucodon*, as a new host of *Moniliformis moniliformis*. The acanthocephalid parasite was extracted from the small intestines of two individuals of Lesser mole-rats. Also, *Heligmosomum spalacis* was found in the host. The study has conducted near Hajdubagos village, Hajdu-Bihar, in Hungary.

Nadtochii (1970), during a study of helminth parasites of rodents in far eastern Russia, the author described *Heligmosomum myospalaxi* Nadtochii, 1970 obtained from the small intestine of *Myospalax myospalax* collected from the seashore of eastern Russia.

Wertheim and Nevo (1971), during a study of helminths of birds and mammals from Israel recovered several species of helminth parasites from the Middle East blind mole-rat, *Nannospalax ehrenbergi* Nehring, 1898 including *Ganguleterakis spalaxi*, *Gongylonema longispiculum* Schulz, 1927, *Trichuris muris* (Schrank, 1788), and one unidentified nematode in the genus *Heligmonella* Mönnig, 1927. They also described *Heligmonina nevoi* Wertheim & Nevo, 1971 from the same host species.

Sharpilo (1973) described *Longistriata spalacis* from the small intestine of Lesser mole-rat, *Nannospalax leucodon*. He reported that this nematode species was also found from *Spalax arenarius* Reshetnik, 1939, and *Spalax microphthalmus*. These specimens were all collected from Ukraine.

Table 3. Endoparasite species diversity of Palearctic subterranean rodents and their known original hosts. Authorities are given for parasite and host species.

Host species	Parasite species	References
Cannomys bodius (Hodgson, 1841)	*Hymenolepis diminuta* (Rudolphi, 1819)	Malsawmtluangi and Tandon 2009
Ellobius fuscocapillus (Blyth, 1843)	*Syphacia obvelata* (Rudolphi, 1802)	Arzamani et al. 2017
Ellobius lutescens Thomas, 1897	*Eimeria lutescenae* Musaev & Veisov, 1963	Musaev and Veisov 1965a
Ellobius talpinus (Pallas, 1770)	*Aprostatandrya macrocephala* Douthitt, 1915	Tokobaev 1960
	Catenotaenia pusilla Goeze, 1782	Zanina and Tokobaev 1962a
	Echinococcus multilocularis Leuckart, 1863	Tokobaev 1960
	Eimeria ellobii Svanbaev, 1965	Musaev and Veisov 1965a
	Eimeria kazakhstanensis Levine, 1965	Levine and Ivens 1965
	Eimeria tadshikistanica Veisov, 1964	Musaev and Veisov 1965a
	Eimeria talpini Levine, 1965	Levine and Ivens 1965
	Hymenolepis diminuta (Rudolphi, 1819)	Zanina and Tokobaev 1962a
	Mesocestoides Vaillant, 1863	Tokobaev 1960
	Moniliformis moniliformis Bremser, 1811	Zanina and Tokobaev 1962a
	Nomadolepis ellobii Makarikov et al., 2010	Makarikov et al. 2010
	Physocephalus ellobii Schulz, 1927	Schultz 1927
	Hydatigera (syn. *Taenia*) *taeniaeformis* (Batsch, 1786)	Zanina and Tokobaev 1962a
Ellobius tancrei Blasius, 1884	*Arostrilepis batsaikhani* Dursahinhan et al., 2022	Dursahinhan et al. 2022
	Echinococcus multilocularis Leuckart, 1863	Afonso et al. 2015
Eospalax baileyi (Thomas, 1911)	*Eimeria baileyii* Cao et al., 2014	Cao et al. 2014
	Eimeria fani Cao et al., 2014	Cao et al. 2014
	Eimeria menyuanensis Cao et al., 2014	Cao et al. 2014
	Eimeria myospalacensis Cao et al., 2014	Cao et al. 2014
	Ransomus qinghaiensis Ming et al., 2004	Ming et al. 2004
	Versteria (syn. *Taenia*) *mustelae* Gmelin, 1790	Zhao, et al. 2014
Eospalax fontanierii (Milne-Edwards, 1867)	*Echinococcus multilocularis* Leuckart, 1863	Craig 2006
	Heligmoptera giraudouxi Elias et al., 2002	Elias, et al. 2002
	Heligmoptera querei Elias et al., 2002	Elias, et al. 2002
Myospalax myospalax (Laxmann, 1773)	*Echinococcus multilocularis* Leuckart, 1863	Shaykenov and Mahmutov 1968
	Heligmoptera sibirica Shakhmatova, 1990	Shakhmatova 1990
	Heligmosomum myospalaxi Nadtochii, 1970	Nadtochii 1970
	Hymenolepis rymzhanovi Makarikov & Tkach, 2013	Makarikov and Tkach 2013
	Moniliformis clarki (Ward, 1917)	Vlasenko and Krivopalov 2017
	Paranoplocephala Lühe, 1910	Vlasenko and Krivopalov 2017
	Versteria mustelae (Gmelin, 1790)	Vlasenko and Krivopalov 2017
Myospalax psilurus (Milne-Edwards, 1874)	*Ascarops strongylina* (Rudolphi, 1819)	Ganzorig et al. 1999
Nannospalax ehrenbergi Nehring, 1898	*Eimeria adiyamanensis* Sayin, 1980	Sayın 1980
	Eimeria anzanensis Couch et al, 1993	Couch et al. 1993
	Eimeria carmelensis Couch et al, 1993	Couch et al. 1993
	Eimeria celebii Sayin, 1980	Sayın 1980
	Eimeria haranica Sayin, 1980	Sayın 1980
	Eimeria marasensis Sayin, 1980	Sayın 1980
	Eimeria microspalacis Golemansky & Darawish, 1992	Golemansky and Darwish 1992
	Eimeria oytuni Sayin, 1980	Sayın 1980
	Eimeria spalacensis Couch et al, 1993	Couch et al. 1993
	Eimeria torosicum Sayin, 1980	Sayın 1980
	Eimeria urfensis Sayin, 1980	Sayın 1980
	Ganguleterakis spalaxi Kozlov & Yangolenko, 1963	Wertheim and Nevo 1971
	Gongylonema longispiculum Schulz, 1927	Wertheim and Nevo 1971
	Heligmonella Mönnig, 1927	Wertheim and Nevo 1971
	Heligmonina nevoi Wertheim & Nevo, 1971	Wertheim and Nevo 1971
	Isospora spalacensis Couch et al, 1993	Couch et al. 1993
	Microcephaloides nevoi (Fair et al., 1990) Haukisalmi 2009	Fair et al. 1990; Haukisalmi 2009
	Trichuris muris (Schrank, 1788)	Wertheim and Nevo 1971

Host species	Parasite species	References
Nannospalax leucodon (Nordmann, 1840)	*Aprostatandrya* Kirshenblat, 1938	Andreiko 1963a
	Ascaris spalacis Shults & Aloyan, 1950	Shults and Aloyan 1950
	Coenurus parviuncinatus Kirschenblatt, 1939	Korniushin and Sharpilo 1986
	Eimeria celebii Sayin, 1980	Nalbantoğlu et al. 2010
	Eimeria elliptica Sayin et al., 1977	Sayin et al. 1977
	Eimeria lalahanensis Sayin, et al., 1977	Sayin et al. 1977
	Eimeria leucodonica Veisov, 1975	Veisov 1975
	Eimeria maralikiensis Veisov, 1975	Veisov 1975
	Eimeria oytuni Sayin, 1980	Nalbantoğlu et al. 2010
	Eimeria spalacis Sayin et al., 1977	Sayin et al. 1977
	Eimeria talikiensis Veisov, 1975	Veisov 1975
	Eimeria torosicum Sayin, 1980	Nalbantoğlu et al. 2010
	Eimeria turkmenica Sayin et al., 1977	Sayin et al. 1977
	Eimeria tuzdili Sayin, et al., 1977	Sayin et al. 1977
	Heligmosomum spalacis Kirsenblat, 1965	Mészáros 1968
	Heligmosomum moldovensis Andreiko, 1963	Andreiko 1963a
	Isospora anatolicum Sayin, et al., 1977	Sayin et al. 1977
	Longistriata spalacis Sharpilo, 1973	Sharpilo 1973a
	Mammalakis spalacis Marcu, 1930	Andreiko 1963a
	Moniliformis moniliformis Bremser, 1811	Murai 1968
	Taenia straminea (Goeze, 1782) Spasskii 1954	Andreiko 1963a
Prometheomys schaposchnikowi Satunin, 1901	*Dicrocoelium dendriticum* (Rudolphi, 1819)	Razumova 1957
	Heligmosomum halli (Schulz, 1926)	Razumova 1957
	Microcephaloides Haukisalmi et al., 2008	Razumova 1957
	Taenia polyacantha Leuckart, 1856	Razumova 1957
	Hydatigera (syn. *Taenia*) *taeniaeformis* (Batsch, 1786)	Razumova 1957
Rhizomys pruinosus (Blyth, 1851)	*Mammalakis spumosa* (Schneider, 1866)	Chaisiri et al. 2017
Rhizomys sinensis Gray, 1831	*Cryptosporidium occultus* Kváč, 2018	Wei et al. 2019
	Cryptosporidium parvum Tyzzer, 1912	Wei et al. 2019
Spalax arenarius Reshetnik, 1939	*Longistriata spalacis* Sharpilo, 1973	Sharpilo 1973a
Spalax graecus Nehring, 1898	*Heligmosomum spalacis* Kirsenblat, 1965	Kirshenblat 1965a
Spalax microphthalmus Güldenstädt, 1770	*Ganguleterakis spalaxi* Kozlov & Yangolenko, 1963	Kozlov and Yangolenko 1963a
	Gongylonema longispiculum spalacis Schulz, 1927	Schultz 1927
	Longistriata spalacis Sharpilo, 1973	Sharpilo 1973a
	Mammalakis spalacis Marcu, 1930	Marcu 1930
	Hydatigera (syn. *Taenia*) *taeniaeformis* (Batsch, 1786)	Sharpilo 1976
	Trichuris spalacis (Petrov & Potechina, 1953)	Petrov and Potechina 1953

Sharpilo (1976), during a study of helminth parasites of rodent fauna in Ukraine, reported *Hydatigera* (syn. *Taenia*) *taeniaeformis* from *Spalax microphthalmus*.

Veisov (1975) described three new species of coccidia of the genus *Eimeria* Schneider, 1875 from *Nannospalax leucodon*, including *Eimeria maralikiensis* Veisov, 1975 and *Eimeria talikiensis* Veisov, 1975 collected from Talnisk and Maralik Aniisk regions, Armenian, also, describing *Eimeria leucodonica* Veisov, 1975 from the Talinsk region only.

Sayin et al. (1977), during a survey of Lesser mole-rats, *Nannospalax leucodon*, in Lalahan district in Ankara, Turkey, described six new species of coccidia in the genus *Eimeria* Schneider, 1875 including *E. elliptica* Sayin et al., 1977, *E. lalahanensis* Sayin et al., 1977, *E. spalacis* Sayin et al., 1977, *E. turkmenica* Sayin et al., 1977, *E. tuzdili* Sayin et al., 1977, and *Isospora anatolicum* Sayin et al., 1977.

Sayın (1980), during a survey conducted from 1976 through 1978, studied 41 individuals of the Middle East blind mole-rats, *Nannospalax ehrenbergi*, from Urfa, Adiyaman, and Maras provinces in Turkey. As a result, seven new species of coccidia of the genus *Eimeria* Schneider, 1875 were described. Those include *E. adiyamanensis* Sayın, 1980, *E. celebii* Sayın, 1980, *E. haranica* Sayın, 1980, *E. marasensis* Sayın, 1980, *E. oytuni* Sayın, 1980, *E. torosicum* Sayın, 1980, and *E. urfensis* Sayın, 1980.

Korniushin and Sharpilo (1986) reported a larval *Taenia* which they reported as *Coenurus parviuncinatus* Kirschenblatt, 1939 obtained from *Nannospalax leucodon* collected from Armenia.

Fair et al. (1990) described a new species of tapeworm, *Microcephaloides nevoi* Fair et al., 1990 from the Middle East blind mole-rat *Nannospalax ehrenbergi* in Masada, Golan Heights, Israel. This species has been redescribed by Haukisalmi (2009).

Shakhmatova (1990) described *Heligmoptera sibirica* Shakhmatova, 1990 found from the Siberian zokor, *Myospalax myospalax*, collected from the Gorno-Altai autonomous region of Russia.

Golemansky and Darwish (1992) described *Eimeria microspalacis* Golemansky & Darwish, 1992 from the Middle East blind mole-rat, *Nannospalax ehrenbergi*, collected from the regions of Damascus and Latakia, western Syria.

Couch et al. (1993) described four coccidian parasites obtained from the Middle East blind mole-rat, *Nannospalax ehrenbergi*, collected from 12 different localities in Israel including *Eimeria anzanensis* Couch et al., 1993, *E. carmelensis* Couch et al., 1993, *E. spalacensis* Couch et al., 1993, and *Isospora spalacensis* Couch et al., 1993.

Ganzorig et al. (1999) redescribed *Ascarops strongylina* (Rudolphi, 1819) from the Transbaikal zokor, *Myospalax psilurus* (Milne-Edwards, 1874) collected from near the Halh Gol River, Dornod province, eastern Mongolia.

Elias et al. (2002), during a joint program of French, British, and China on echinococcosis screening in Zhang County, China (Gansu), two new species of *Heligmoptera* Nadtochiy, 1977 were described from the small intestines of the Chinese zokor, *Eospalax fontanierii* (Milne-Edwards, 1867) including: *Heligmoptera giraudouxi* Elias & Durette-Desset, 2002, and *Heligmoptera querei* Elias & Durette-Desset, 2002 with the new description of the genus.

More recently in China, Ming et al. (2004) described *Ransomus qinghaiensis* Ming et al., 2004 from the cecum of the Plateau zokor, *Eospalax baileyi* (Thomas, 1911) collected from Qilian County, Qinghai province.

Craig (2006), in a survey and epidemiological assessment of human alveolar echinococcosis in 33 provinces of China, listed the Chinese zokor, *Eospalax fontanierii* as one of the intermediate hosts of *Echinococcus multilocularis*.

Malsawmtluangi and Tandon (2009) reported *Hymenolepis diminuta* attained from the Lesser bamboo rat, *Cannomys bodius* (Hodgson, 1841) collected from Mizoram, northeast India.

Nalbantoğlu et al. (2010) reported three species of coccidia acquired from the feces of the Lesser mole-rat, *Nannospalax leucodon*, collected from the Eryaman district of Ankara, Turkey. Those are *Eimeria* celebii, *E. oytuni* Sayin, 1980, and *E. torosicum* Say-

in, 1980. In the same year, Makarikov et al. (2010) described the cestode *Nomadolepis ellobii* Makarikov et al., 2010, simultaneously establishing a new genus for the tapeworm that was obtained from the small intestine of the Northern mole vole, *Ellobius talpinus*, collected from southwestern Siberia, Russia.

Soon after, Makarikov and Tkach (2013) described *Hymenolepis rymzhanovi* Makarikov & Tkach, 2013 from the small intestine of the Siberian zokor, *Myospalax myospalax* collected from eastern Kazakhstan.

Cao et al. (2014) described four new species of *Eimeria* from the Plateau zokor, *Eospalax baileyi*, collected from Haibei area, Qinghai Province, China. The parasites include *Eimeria baileyii* Cao et al., 2014, *Eimeria fani* Cao et al., 2014, *Eimeria menyuanensis* Cao et al., 2014, and *Eimeria myospalacensis* Cao et al., 2014. In the same year, Zhao et al. (2014) identified *Versteria* (syn. *Taenia*) *mustelae* (Gmelin, 1790) using DNA sequencing of larval cysts found in the Plateau zokor, *Eospalax baileyi* collected from Datong County, east of Qinghai province, China. In this study, no data were provided on number of individuals infected.

Afonso et al. (2015) reported *Echinococcus multilocularis* from the livers of Eastern mole voles, *Ellobius tancrei* which acts as the intermediate host for this cestode, collected from Sary Mogol, Alay valley, Kyrgyzstan. The authors also noted that the definitive hosts were local domestic dogs, whose feces were examined for *E. multilocularis*. The parasite samples from the dogs were genetically identical to those found in the intermediate host.

In 2017, a flurry of activity resulted from workers in the field. Vlasenko and Krivopalov (2017) reported *Moniliformis clarki* (Ward, 1917), *Paranoplocephala* Lühe, 1910 and larvae of *Versteria mustelae* (Gmelin, 1790) from *Myospalax myospalax* collected from the southern Tomsk region, Russia. Then, Arzamani et al. (2017) reported *Syphacia obvelata* (Rudolphi, 1802) (probably a misidentification as *S. obvelata* occurs only in species of *Mus*) obtained in the Southern mole vole, *Ellobius fuscocapillus* (Blyth, 1843), collected from north Khorasan province of northeast Iran. Finally in 2017, Chaisiri et al. (2017), during an ecological study of host-parasite associations, reported *Mammalakis spumosa* (Schneider, 1866) from *Rhizomys pruinosus* in Cambodia.

Wei et al. (2019) reported *Cryptosporidium parvum* Tyzzer, 1912 and *C. occultus* Kváč, 2018 found in the Chinese bamboo rat, *Rhizomys sinensis*, collected from south-central China.

Dursahinhan et al. (2022) described *Arostrilepis batsaikhani* from the Zaisan mole vole, *Ellobius tancrei* collected from Baitag Bogd, Hovd province, western Mongolia.

Endoparasites of Nearctic and northern Neotropical subterranean rodents

See graphical summary in Fig. 3 and endoparasite list Table 4.

Leidy in (1857), at a meeting of the Academy of Natural Sciences of Philadelphia, displayed some warbles taken from an evidently incapacitated pocket gopher by the side of the road, identified as *T. borealis* [probably a synonym of *T. talpoides*] near

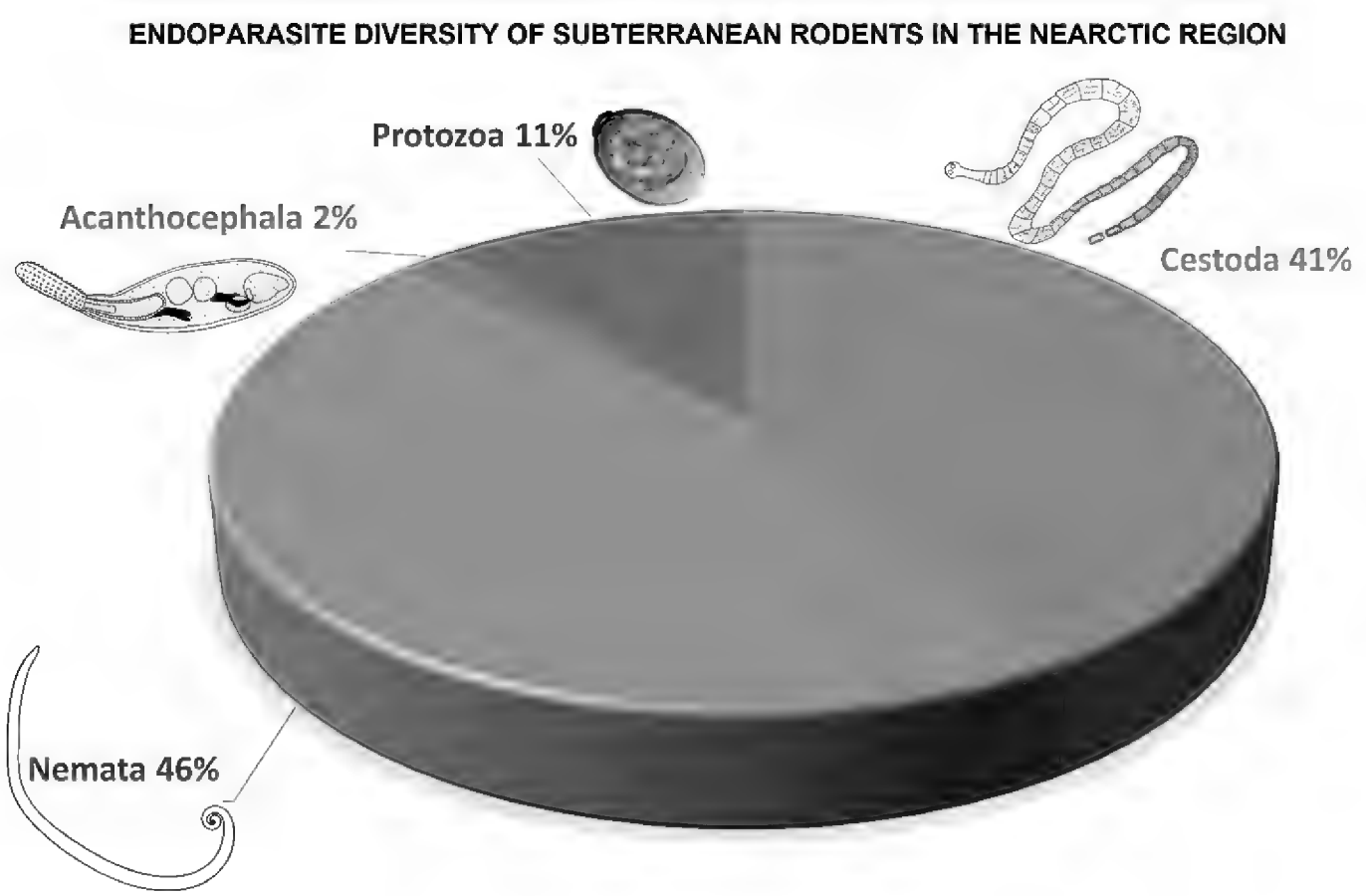

Figure 3. Percentage taxon composition pie diagram of the higher classification of endoparasite diversity occurring in Nearctic subterranean rodents (Family Geomyidae) derived from literature records published from 1857 through 2020. Among these endoparasites, the Nemata represent 46% of the species found followed by Cestoda (41%), Protozoa (11%), and Acanthocephala at just 2%.

the Bridger's pass summit of the Rocky Mountains. This record represents the first known report of an endoparasite from a member of the rodent family Geomyidae. Soon after the groundbreaking work by Leidy, Charles Wardell Stiles (1895) reported the first helminth parasite from a geomyid when he described *Pseudocittotaenia praecoquis* (Stiles, 1895) from *Geomys bursarius* (Shaw, 1800) collected near Ames, Iowa (Stiles, 1897).

Hall (1912) reported on the parasite fauna of Colorado and recorded several nematodes and some unidentified cestodes from *Thomomys fossor* J.A. Allen (probably a syn. of *T. talpoides*). Soon after, Herman Douthitt (1915) described four new species of anoplocephalid cestodes from pocket gophers collected from the central United States. *Anoplocephaloides variabilis* (Douthitt, 1915), *A. infrequens* (Douthitt, 1915), and *Andrya macrocephala* Douthitt, 1915 were all described from specimens taken from *G. bursarius* collected from Illinois, Minnesota, and North Dakota. *Monoecocestus anoplocephaloides* (Douthitt, 1915) was described from some specimens taken from *Geomys breviceps* Baird collected near Norman, Oklahoma. Douthitt (1915) also reported one unidentified species of *Oöchoristica* Luhe, 1898, and one immature form of *Cittotaenia*, now known as *Pseudocittotaenia*, Tenora, 1976 from *G. bursarius*. Douthitt (1915) also reported numerous individuals of eight different species of *Hymenolepis* from two species of pocket gophers including: *G. bursarius* collected in Illinois,

Wisconsin, Minnesota, North Dakota, and Manitoba, Canada; *G. breviceps* collected in Oklahoma and Texas; and *Geomys personatus* True, collected in Texas.

Hall (1916) described the following nematodes from *Thomomys fossor* J. A. Allen [syn. *T. talpoides* (Richardson, 1828)]: *Trichuris fossor* Hall, 1916, from specimens collected near both Crested Butte and Livermore, Colorado and *Vexillata vexillata* (Hall, 1916) from gophers collected from mountain meadows near Livermore, Colorado. These nematodes were described from the same material that Hall (1912) had previously studied. Additionally, the nematode *Protospirura ascaroidea* Hall, 1916 was described from specimens recovered from the stomachs of *Geomys bursarius* collected near Norman, Oklahoma by Herman Douthitt and sent to MC Hall for study.

Skidmore (1929) described a species of Coccidia named *Eimeria geomydis* Skidmore, 1929 from the intestinal tract of *Geomys bursarius* Shaw, collected near Lincoln, Nebraska while Dikmans (1932) reported *Capillaria* (syn. *Calodium*) *hepaticum* (Bancroft, 1893) as a parasite of *Thomomys fossor* (syn. *T. talpoides*) collected in the Medicine Bow Mountains of Wyoming. In that same year, English (1932) examined 161 specimens of *Geomys bursarius* collected in Brazos County, Texas and found 23 infected with the stomach nematode *Protospirura ascaroidea* Hall, 1916, and eight infected with an unknown species of *Hymenolepis*.

Hubbell and Goff (1939) reported *Mastophorus muris ascaroides* (Gmelin, 1790) to occur commonly in the stomach of *Geomys* sp. (most likely *G. pinetis*) collected near Leesburg, Lake County, Florida.

McIntosh (1941) described *Catenotaenia linsdalei* McIntosh, 1941 from *Thomomys bottae bottae* (Eydoux & Gervais, 1836) collected near Monterey, California on the Hastings Natural History Reservation.

Caballero and Cerecero (1943) described *Vexillata convoluta* from the small intestine of the Merriam's pocket gopher, *Cratogeomys merriami* (Thomas, 1893), collected from the state of Michoacan, Mexico.

Chandler (1945) redescribed *Trichuris fossor* Hall, 1916 from *Thomomys bottae bottae* from specimens collected on the Hastings Natural History Reservation near Monterey, California. This was the first good description of the eggs of *T. fossor*, and the first report of *T. fossor* from *T. bottae*. In the same year during an ecological study of the small mammals collected from Northrup Canyon in eastern Washington State, Rankin (1945) recorded *Hymenolepis diminuta* (Rudolphi, 1819) from *Thomomys talpoides*, see discussion below. The next year, Wenrich (1946) recorded a species of *Monocercomonoides* Travis, 1932 as a cecal commensal (flagellate) of Botta's pocket gopher, *Thomomys bottae*.

Tryon (1947) reported both cestodes and nematodes in *Thomomys talpoides* from Montana, with most of his field work occurring in the Bridger Mountains. Less than one percent of the gophers necropsied contained an unidentified species of cestode. Nematodes identified as belonging to the family Trichuridae were found in 100% of the pocket gophers examined for endoparasites. In areas of low pocket gopher density, the prevalence of infection was low (approximately 10%); however, in areas of high gopher density, the prevalence of infection approached 80%. Tryon (1947) speculated that the young

Table 4. Endoparasite species diversity of Nearctic and Neotropical regions of subterranean rodents in the family Geomyidae and their known hosts. Authorities are given for parasite and host species. The new host-parasite associations recorded in this work are denoted by 'Present study' in bold.

Host species	Parasite species	References
Cratogeomys castanops (Baird, 1852)	*Calodium americanum* (Read, 1949)	**Present study**
	Eimeria geomydis Skidmore, 1929	**Present study**
	Monoecocestus sp. Beddard, 1914	**Present study**
	Vexillata convoluta Caballero & Cerecero, 1943	**Present study**
Cratogeomys merriami (Thomas, 1893)	*Paraspidodera uncinata* Travassos, 1914	Lamothe-Argumedo et al. 1997
	Vexillata convoluta Caballero & Cerecero, 1943	Caballero and Cerecero 1943
Cratogeomys planiceps (Merriam, 1895)	*Hymenolepis cratogeomyos* Gardner et al., 2020	Gardner et al. 2020
Geomys attwateri Merriam, 1895	*Monoecocestus centroovarium* Dronen et al., 1994	Dronen et al. 1994
	Protospirura ascaroidea Hall, 1916	LeBrasseur 2017
	Vexillata geomyos Falcón-Ordaz et al., 2006	Falcón-Ordaz et al. 2006
Geomys breviceps Baird, 1855	*Eimeria geomydis* Skidmore, 1929	Upton et al. 1992
	Litomosoides westi Gardner & Schmidt, 1986	Pitts et al. 2000
	Monoecocestus anoplocephaloides (Douthitt, 1915)	Douthitt 1915
	Protospirura ascaroidea Hall, 1916	Hall 1916; English 1932
Geomys bursarius (Shaw, 1800)	*Andrya macrocephala* Douthitt, 1915	Douthitt 1915; Hansen 1950; Ubelaker and Downhower 1965; Bartel and Gardner 2000
	Anoplocephaloides infrequens (Douthitt, 1915)	Douthitt 1915; Ubelaker and Downhower 1965; Bartel and Gardner 2000; Rausch 1976
	Anoplocephaloides variabilis (Douthitt, 1915)	Douthitt 1915; Rausch 1976
	Calodium americanum (Read, 1949)	Bartel and Gardner 2000
	Calodium hepaticum (Bancroft, 1893)	Ubelaker and Downhower 1965
	Cittotaenia perplexa Stiles, 1897	Burnham 1953
	Eimeria geomydis Skidmore, 1929	Skidmore 1929; Levine and Ivens 1965
	Hymenolepis diminuta (Rudolphi, 1819)	Burnham 1953
	Hymenolepis geomydis Gardner & Schmidt, 1988	Gardner and Schmidt 1988
	Hymenolepis weldensis Gardner & Schmidt, 1988	Gardner and Schmidt 1988; Bartel and Gardner 2000; Haukisalmi et al. 2010
	Litomosa filaria (Beneden, 1873)	Burnham 1953
	Litomosoides westi Gardner & Schmidt, 1986	Gardner and Schmidt 1986
	Moniliformis clarki (Ward, 1917)	Bartel and Gardner 2000
	Monocercomonoides Travis, 1932	Rissky 1962
	Monoecocestus anoplocephaloides (Douthitt, 1915)	Burnham 1953
	Oochoristica Lűhe, 1898	Douthitt 1915
	Ostertagia Ransom, 1907	Burnham 1953
	Paranoplocephala infrequens (Douthitt, 1915)	Ubelaker and Downhower 1965
	Physaloptera limbata Leidy, 1856	Bartel and Gardner 2000
	Protospirura ascaroidea Hall, 1916	English 1932; LeBrasseur 2017
	Protospirura muris ascaroides (Hall, 1916)	Burnham 1953
	Pseudocittotaenia praecoquis (Stiles, 1985)	Stiles 1895
	Ransomus rodentorum Hall, 1916	Bartel and Gardner 2000
Geomys jugossicularis Hooper, 1940	*Anoplocephaloides variabilis* (Douthitt, 1915)	**Present study**
Geomys lutescens Merriam, 1890	*Hymenolepis weldensis* Gardner & Schmidt, 1988	Gardner et al. 2020
	Litomosoides westi Gardner & Schmidt, 1986	**Present study**
	Physaloptera limbata Leidy, 1856	**Present study**
	Ransomus rodentorum Hall, 1916	**Present study**
	Monoecocestus anoplocephaloides (Douthitt, 1915)	Burnham 1953
Geomys personatus True, 1889	*Litomosoides westi* Gardner & Schmidt, 1986	Pitts et al. 2000
	Protospirura ascaroidea Hall, 1916	LeBrasseur 2017
Geomys pinetis Rafinesque, 1817	*Mastophorus muris ascaroides* (Gmelin, 1790)	Hubbell and Goff 1939
Geomys texensis Merriam, 1895	*Eimeria geomydis* Skidmore, 1929	Upton et al. 1992
	Hymenolepis Weinland, 1858	LeBrasseur 2017
	Protospirura ascaroidea Hall, 1916	LeBrasseur 2017
Heterogeomys heterodus (Peter, 1865)	*Hobergia irazuensis* Gardner et al., 2020	Gardner et al. 2020
Orthogeomys grandis (Thomas, 1893)	*Eimeria orthogeomys* Lainson, 1968	Lainson 1968

Host species	Parasite species	References
Thomomys bottae (Eydoux & Gervais, 1836)	*Arostrilepis horrida* (von Linstow, 1901)	Schiller 1952; Voge 1955; Gardner 1985
	Catenotaenia dendritica (Goeze, 1782)	Voge 1955
	Catenotaenia linsdalei McIntosh, 1941	McIntosh 1941
	Eimeria thomomysis Levine et al., 1957	Levine et al. 1957; Levine and Ivens 1965
	Heligmosomoides thomomyos Gardner & Jasmer, 1983	Gardner and Jasmer 1983
	Hymenolepis citelli (McLeod, 1933)	Voge 1955; Jasmer 1980
	Litomosoides thomomydis Gardner, 1986	Gardner and Schmidt 1986
	Monocercomonoides Travis, 1932	Gardner and Jasmer 1983
	Monoecocestus anoplocephaloides (Douthitt, 1915)	Hansen 1950
	Ransomus rodentorum Hall, 1916	Jasmer 1980
	Trichuris fossor Hall, 1916	Jasmer 1980; Douglas 1969
Thomomys bulbivorus (Richardson, 1829)	*Arostrilepis horrida* (von Linstow, 1901)	Gardner 1985
	Arostrilepis schilleri Makarikov et al., 2012	Makarikov et al. 2012
	Heligmosomoides thomomyos Gardner & Jasmer, 1983	Gardner 1985; Gardner and Jasmer 1983
	Hymenolepis tualatinensis Gardner, 1985	Gardner 1985
	Ransomus rodentorum Hall, 1916	Gardner 1985
	Trichuris fossor Hall, 1916	Gardner 1985
Thomomys clusius Coues, 1875	*Ransomus rodentorum* Hall, 1916	**Present study**
	Trichuris fossor Hall, 1916	**Present study**
Thomomys monticola J. A. Allen, 1893	*Arostrilepis horrida* (von Linstow, 1901)	Howard and Childs 1959
	Trichuris Roederer, 1761	Ingles 1952
Thomomys talpoides (Richardson, 1828)	*Andrya macrocephala* Douthitt, 1915	Rausch and Schiller 1949
	Anoplocephaloides infrequens (Douthitt, 1915)	Frandsen and Grundmann 1961; Todd et al. 1971
	Anoplocephaloides variabilis (Douthitt, 1915)	Rausch 1976; Frandsen and Grundmann 1961; Todd et al. 1971; Lubinsky 1957
	Arostrilepis horrida (von Linstow, 1901)	Grundmann, et al. 1976; Frandsen and Grundmann 1961
	Ascaris laevis Leidy, 1856	Grundmann et al. 1976; Frandsen and Grundmann 1961
	Calodium hepaticum (Bancroft, 1893)	Ubelaker and Downhower 1965; Lubinsky 1957; Dikmans 1932; Tryon 1947; Lubinsky 1956; Rausch 1961; Tryon and Cunningham 1968
	Catenotaenia linsdalei McIntosh, 1941	Todd et al. 1971
	Eimeria fitzgeraldi Todd & Tryon, 1970	Todd et al. 1971; Todd and Tryon 1970
	Eimeria jemezi Wilber et al., 1994	Wilber et al. 1994
	Eimeria thomomysis Levine et al., 1957	Levine and Ivens 1965; Levine et al. 1957
	Hymenandrya thomomyis Smith, 1954	Smith 1954
	Hymenolepis citelli (McLeod, 1933)	Frandsen and Grundmann 1961
	Hymenolepis diminuta (Rudolphi, 1819)	Rankin 1945
	Litomosoides carinii (Travassos, 1919)	Lubinsky 1957
	Litomosoides thomomydis Gardner, 1986	Gardner and Schmidt 1986
	Nippostrongylus muris (Yokogawa, 1920)	Frandsen and Grundmann 1961
	Protospirura ascaroidea Hall, 1916	Todd et al. 1971
	Pseudocittotaenia glandularis Beveridge, 1978	Beveridge 1978
	Pseudocittotaenia praecoquis (Stiles, 1985)	Grundmann et al. 1976; Frandsen and Grundmann 1961; Smith 1951
	Ransomus rodentorum Hall, 1916	Grundmann et al. 1976; Frandsen and Grundmann 1961
	Trichuris fossor Hall, 1916	Hall 1916; Grundmann et al. 1976; Frandsen and Grundmann 1961; Lubinsky 1957; Todd and Lepp 1972
	Versteria mustelae (Gmelin, 1790)	Lubinsky 1957
	Vexillata vexillata (Hall, 1916)	Todd et al. 1971
Thomomys umbrinus (Richardson, 1829)	*Arostrilepis horrida* (von Linstow, 1901)	Frandsen and Grundmann 1961
	Ascaris laevis Leidy, 1856	Frandsen and Grundmann 1961
	Hymenolepis citelli (McLeod, 1933)	Frandsen and Grundmann 1961
	Moniliformis clarki (Ward, 1917)	Frandsen and Grundmann 1961
	Paruterina candelabraria (Goeze, 1782)	Frandsen and Grundmann 1961
	Ransomus rodentorum Hall, 1916	Frandsen and Grundmann 1961
	Trichuris fossor Hall, 1916	Frandsen and Grundmann 1961

gophers became infected before leaving the parental burrows, and by August, the prevalence of infection for the young pocket gophers was ca. 50%. Nematodes, probably of the genus *Protospirura* were found in the stomachs of some gophers, with as many as 42 in an individual pocket gopher's stomach. Concerning the presence of warbles in the pocket gophers examined during the study, Tryon stated "only 15 out of over a thousand animals examined showed warbles. Of these, ten were juveniles indicating that they may be above ground more than the adults, probably during migration from the parental burrows."

Rausch and Schiller (1949), during a study of cestodes of the genus *Andrya* Railliet, 1893, mentioned *Andrya macrocephala* Douthitt, 1915 as occurring in *Thomomys talpoides tenellus* Goldman from the Jackson Hole Wildlife Park in Wyoming.

Hansen (1950), during a study of the tapeworms of rodents, recorded *Andrya macrocephala* Douthitt, 1915 as occurring in 5 of 5 *Geomys bursarius* examined with up to 12 cestodes per host. Hansen (1950) also recorded *Monoecocestus anoplocephaloides* (Douthitt, 1915) from *Thomomys bottae* collected in the region of Sacramento, California. Interestingly, this cestode has not since been reported from any members of the genus *Thomomys*.

Smith (1951), in a study of the cestodes of *Thomomys talpoides* collected from Carbon County, Wyoming, reported the following cestodes: *Pseudocittotaenia praecoquis* (Stiles, 1895) from the small intestine; *P. megasacca* (Smith, 1951) also from the small intestine (see below for clarification of the taxonomy of these two species). Smith (1951) also included a list of the cestodes reported from pocket gophers up to that time and attempted to clarify the taxonomic relationships between *Schizotaenia* Janicki, 1904 and *Monoecocestus* Beddard, 1914.

Ingles (1952) reported *Trichuris* sp. (probably *T. fossor*) as a common parasite of the cecum of *Thomomys monticola* J. A. Allen, 1893. All specimens that Ingles examined came from an elevation of ca. 7,000 feet in the Sierra Nevada of California. In the same year, Everett Schiller (1952), in a study of the morphological variation in *Hymenolepis* (syn. *Arostrilepis*) *horrida* (von Linstow, 1901) reported *Thomomys bottae* from near O'Neals California as a host.

Burnham (1953), during a study of the parasites of *Geomys bursarius*, collected from four counties in Oklahoma reported the following species of parasites: *Protospirura muris ascaroides* (Hall, 1916) (syn. *Mastophorus muris*) from the stomachs of 18 hosts; *Litomosa filaria* Beneden, 1897 from the pleural cavities of 19 gophers (this is probably a misidentification, see discussion below regarding the filarioid nematodes of pocket gophers); *Ostertagia* sp. from the stomachs of five gophers; *Hymenolepis diminuta* (Rudolphi, 1819) from the small intestines of ten hosts (see discussion below for clarification of the problem concerning *H. diminuta* in geomyids); *Monoecocestus anoplocephaloides* (Douthitt, 1915) from 25 hosts, with a range of infection of 1–100 worms per host; and *Cittotaenia perplexa* Stiles, 1897 from two gophers.

Soon after, Smith (1954) described *Hymenandrya thomomyis* from the small intestine of *Thomomys talpoides* collected in Colorado and in this same publication, he recommended that *Catenotaenia linsdalei* McIntosh, 1941 be considered a synonym of *C. dendritica* (Goeze, 1782) Janicki 1904.

Voge (1955) in a catalogue of the cestode parasites of California mammals, listed *Catenotaenia dendritica* (Goeze, 1782), *Hymenolepis citelli* (McLeod, 1933), and an unidentified species of *Hymenolepis* from *T. bottae*.

The next year, Voge (1956), in a list of the nematode parasites of California mammals, reported *Trichuris fossor* Hall, 1916 as a parasite of *T. bottae* and in the same year, Lubinsky (1956) reported *Calodium* (syn. *Capillaria*) *hepaticum* from *T. talpoides* in Alberta, Canada. Soon after, continuing his work on small mammals, Lubinsky (1957) in a list of the helminth parasites of rodents from Alberta included the following as parasites of *Thomomys talpoides*: *Versteria* (syn. *Taenia*) *mustelae* (larvae) from the mesenteries, lungs, liver, and kidneys of gophers collected in northern and middle Alberta: *Anoplocephaloides variabilis* (Douthitt, 1915) recovered from the colon (which is a doubtful location for a cestode) from six localities in middle and southern Alberta; *Calodium* (syn. *Capillaria*) *hepaticum* from the livers of gophers collected from central and southern Alberta; *Trichuris fossor* from the cecum of gophers collected from central Alberta; *Protospirura ascaroidea* Hall, 1916 from the stomachs of gophers from middle Alberta; *Litomosoides carinii* (Travassos, 1919) from the coelom of pocket gophers from middle and southern Alberta. In the same year, Levine, et al. (1957) described *Eimeria thomomysis* from specimens of *T. bottae* collected in the Grand Canyon of Arizona.

Howard and Childs (1959) during a study of the ecology of *Thomomys monticola* reported *Hymenolepis horrida* (von Linstow, 1901) to occur commonly in adult pocket gophers. They stated, "Most of the adults had several tapeworms (*Hymenolepis horrida*), and one animal had 108 immature tapeworms with short strobila. None of the five juvenile gophers examined had tapeworms." Based on recent work by Dursahinhan et al. (2022), it appears now that the species identified as *H. horrida* may be referred to the genus *Arostrilepis*.

Frandsen and Grundmann (1960) discussed the geographic distribution of *Trichuris fossor* Hall, 1916 and *Ransomus rodentorum* Hall, 1916 from *Thomomys talpoides* and *T. umbrinus* in the Lake Bonneville basin of Utah. They speculated that the distribution of these two species of nematodes in *Thomomys* sp. in this area supports the contention that competition occurred between the two species of pocket gophers resulting in the present-day distribution patterns of the pocket gophers and their respective helminths.

Rausch (1961) reported *Calodium* (syn. *Capillaria*) *hepaticum* from *Thomomys talpoides tenellus* Goldman from near Moran, Wyoming, collected in June of 1948 and Frandsen and Grundmann (1961) reported the following helminth parasite species from several subspecies of both Northern pocket gopher, *Thomomys talpoides*, and the Southern pocket gopher *Thomomys umbrinus* (Richardson, 1829). These species include *Ascaris laevis* Leidy, 1856, *Hymenolepis citelli*, *Ransomus rodentorum*, and *Trichuris fossor*. However, *Anoplocephaloides infrequens* (Douthitt, 1915), *A. variabilis* (Douthitt, 1915), *Pseudocittotaenia praecoquis* (Stiles, 1985), *Arostrilepis horrida*, and *Nippostrongylus muris* (Yokogawa, 1920) have been reported from *T. talpoides*. In addition, *Paruterina candelabraria* (Goeze, 1781) and *Moniliformis clarki* are only reported from *T. umbrinus*.

Stock (1962) reported three males and one female of the nematode *Ransomus rodentorum* from the cecae of two specimens of *Thomomys talpoides fossor*, collected at the junction of Dry Gulch and the Gunnison River, Colorado, at ca. 7,400 feet altitude.

Rissky (1962) reported *Monocercomonoides* from the cecum of the Plains pocket gopher, *Geomys bursarius*, collected from Clay County, South Dakota.

Ubelaker and Downhower (1965) in a study of the endo and ectoparasites of *Geomys bursarius* in Kansas, reported *Calodium* (syn. *Capillaria*) *hepaticum* from the cecum of a single pocket gopher and *Andrya macrocephala* Douthitt, 1915 and *Anoplocephaloides infrequens* (Douthitt, 1915) were found to occur in seven and six of the pocket gophers examined, respectively.

Lainson (1968), during a parasitological study in El Cayo District British Honduras, a new species of coccidian parasite (*Eimeria orthogeomyos*) was described from the Giant pocket gopher, *Orthogeomys grandis* (Thomas, 1893) collected from Baking Pot, El Cayo District, Central America (Lainson, 1968).

Tryon and Cunningham (1968) in a study of *Thomomys talpoides* along an altitudinal transect in the Beartooth Mountains of Wyoming reported *Calodium* (syn. *Capillaria*) *hepaticum* from the livers of 5%, 37%, and 8% of the gophers from the Alpine, the Canadian, and the transition life zones, respectively.

Douglas (1969) studied the ecology of the pocket gophers of Mesa Verde, Colorado. He reported *Trichuris fossor* Hall, 1916 and *Cuterebra* cf. *cyanella* (bot fly larvae) from *Thomomys bottae aureus* Douglas (1969) stated that, "Of the gophers infected with bot fly larvae, the highest prevalence of infection occurred during September, with no gophers carrying larvae during the spring." Douglas (1969) also stated "Specimens of Cestoda currently are being studied and will be reported elsewhere." To our knowledge, no report has ever been published.

Todd and Tryon (1970) described *Eimeria fitzgeraldi* Todd & Tryon, 1970 from *Thomomys talpoides* collected from the Beartooth Mountains, Park County Wyoming. Oocysts were recovered from the feces of two of ten juvenile males and one of 31 adult females (pocket gophers).

Todd et al. (1971) in a study of the endoparasites of the Northern pocket gopher (*Thomomys talpoides*) from Park County, Wyoming, reported the following species of parasites from a total of 46 specimens of *T. talpoides* examined: *Eimeria thomomysis* Levine, Ivens & Kruidenier, 1957 was found to occur in the fecal pellets of 24 of the individual gophers; *E. fitzgeraldi* Todd & Tryon, 1970 was found in the feces of two gophers; cestode cysticerci of the family Taeniidae were found in the mesenteries near the stomach and cecum of one gopher; fragments of the cestode *Catenotaenia linsdalei* McIntosh, 1941 were found in the body cavities of two animals (this is a dubious body location record); *Anoplocephaloides variabilis* (Douthitt, 1915) was present in the small intestines of 18 gophers; *A. infrequens* (Douthitt, 1915) was recovered from the small intestine of seven gophers; *Anoplocephaloides* sp. was recovered from the small intestines of 22 gophers *R. rodentorum* was found in the cecum of 34 gophers, and in the large intestine of one; *Vexillata vexillata* was recovered from the small intestines of two gophers; *Protospirura ascaroidea* was found in the stomachs of two animals;

Trichuris fossor was found in the ceca of 30 gophers; and *Calodium* (syn. *Capillaria*) *hepaticum* was recovered from the livers of 18 of the gophers examined.

Todd and Lepp (1972) redescribed *Trichuris fossor* from specimens recovered from *T. talpoides* from Park County, Wyoming.

Grundmann et al. (1976), in a paper discussing the mechanisms of parasitic helminth population regulation in rodents, listed the following parasites as occurring in *Thomomys talpoides* in Utah: *Trichuris fossor*, *Vexillata vexillata*, *Ascaris laevis* Leidy, 1856. *Hymenolepis horrida*, and *T. fossor* were reported from *T. bottae* in the same paper.

Rausch (1976) in a study of the rodent cestode genera *Paranoplocephala* Luhe, 1910 and *Anoplocephaloides* Baer, 1923 examined the type material of *Anoplocephaloides infrequens* (Douthitt, 1915) from *Geomys bursarius* collected by Douthitt in Brainerd, Minnesota, and specimens of *A. variabilis* (Douthitt, 1915) collected by Douthitt in central Illinois from *Geomys bursarius*. Also studied by Rausch (1976) were seven specimens of *A. variabilis* from *Thomomys talpoides* collected at Emerson, Manitoba, 10 km north of Prince Albert, Saskatchewan, Canada and from 5 km south of Saskatoon, Saskatchewan, Canada. Rausch (1976) stated "I also obtained it (*A. variabilis* from *T. talpoides*) in two of 11 of these rodents at Moran, Wyoming, in 1949."

Beveridge (1978) in a revision of the genus *Pseudocittotaenia* Tenora, 1976, listed the synonyms of *P. praecoquis* (Stiles, 1895) and described *P. glandularis* Beveridge, 1978 from some specimens taken from *Thomomys talpoides* in Utah by Frandsen and Grundmann (1961), and from some specimens from *T. talpoides* in Wyoming. Frandsen and Grundmann (1961) evidently misidentified *P. glandularis* Beveridge, 1978 and had determined that the specimens that they found in *T. talpoides* were *Pseudocittotaenia praecoquis* (Stiles, 1895). The specimens from the Wyoming pocket gophers were from material that Smith (1951) had mistakenly identified and redescribed as *P. praecoquis*. Beveridge (1978) also listed as synonyms: *P. megasacca* (Smith, 1951) with *P. praecoquis* (Stiles, 1895). Also reported by Beveridge (1978) and not reported elsewhere in the literature was *Pseudocittotaenia praecoquis* from *T. talpoides tenellus* Goldman, collected by Robert L. Rausch near Moran, Wyoming in June of 1948.

Jasmer (1980) in a thesis written at Humboldt State University listed the following parasites from *Thomomys bottae* (Eydoux & Gervais): *Ransomus rodentorum*, *Trichuris fossor*, *Hymenolepis citelli*, and an unidentified species of *Heligmosomoides* Hall, 1916. He also discussed the biological characteristics and taxonomy of *R. rodentorum* (some of his specimens are now in the Manter Laboratory Parasite Collection).

Gardner and Jasmer (1983) described *Heligmosomoides thomomyos* Gardner & Jasmer, 1983 from *Thomomys bottae* (Eydoux & Gervais) and *T. bulbivorus* (Richardson) from Humboldt County, California and Benton County, Oregon, respectively. They included some measurements and remeasurements of two other species of *Heligmosomoides*: *H. longispiculatus* (Dickmans, 1940) and *H. montanus* Durette-Desset, 1968.

Gardner (1985) described *Hymenolepis tualatinensis* from the duodenum of the Camas pocket gopher, *Thomomys bulbivorus* (Richardson, 1829) collected near the Tualatin River in the Willamette Valley of Oregon. In the report, several helminth species were documented during the study including *Arostrilepis horrida* also from the small

intestine, *Trichuris fossor* from the cecum, *Ransomus rodentorum* from the cecum, and *Heligmosomoides thomomyos* from the duodenum.

Gardner and Schmidt (1986) described *Litomosoides thomomydis* from the abdominal cavity of the Northern pocket gopher, *Thomomys talpoides*, and Botta's pocket gopher, *Thomomys bottae*, from Huerfano County, Colorado. Also, *L. westi* was described from the abdominal and pleural cavities of the Plains Pocket Gopher, *Geomys bursarius*, collected from Weld County, Colorado.

Shortly after this work, Gardner and Schmidt (1988) described two new species in the genus *Hymenolepis* Weinland, 1858, including *H. weldensis* and *H. geomydis* from the small intestines (duodenum) of the Plains pocket gopher, *Geomys bursarius*, collected from Weld County, Colorado.

Pitts et al. (1990) reported *Litomosoides westi* Gardner & Schmidt, 1986 from *Geomys personatus* True, 1889 collected from Duval and Zapata counties in Texas.

Upton et al. (1992) reported *Eimeria geomydis* Skidmore, 1929 from Baird's pocket gopher, *Geomys mericanu*, and Llano pocket gopher, *Geomys texensis* Merriam, 1895 collected from Texas.

Dronen et al. (1994) described *Monoecocestus centroovarium* found in Attwater's pocket gopher, *Geomys attwateri* Merriam, 1895 collected from Atascosa County, Texas. In the same year, Wilber et al. (1994) described *Eimeria jemezi* found in the Northern pocket gopher, *Thomomys talpoides* collected from El Cajete crater, Jemez Springs, Sandoval County, New Mexico.

Lamothe-Argumedo et al. (1997) reported *Paraspidodera merican* Travassos, 1914 from the intestine of Merriam's pocket gopher, *Cratogeomys merriami* (Thomas, 1893) first collected from Morelos, Cuernavaca, Mexico in 1984.

Pitts et al. (2000) reported the additional occurrence of the filarioid nematode, *Litomosoides westi* from the pleural cavities of Baird's pocket gopher, *Geomys mericanu* collected at the entrance of Isle, Du Boris unit, Lake Ray Roberts State Park, Denton County, Texas while *L. westi* was also documented from the pleural cavities of the Plains pocket gopher, *Geomys bursarius* captured near Aubrey, Grubbs Road, same county.

Bartel and Gardner (2000) reported the helminth parasites from the Plains pocket gopher, *Geomys bursarius*, from seven localities in the northern boundary range, Minnesota. The report includes the following: *Physaloptera limbata* Leidy, 1856 from the stomach, *Ransomus rodentorum* from the cecum and large intestine and *Calodium* (syn. *Capillaria*) *mericanum* (Read, 1949), *Anoplocephaloides infrequens*, *A. variabilis* (Douthitt, 1915), *Andrya macrocephala*, *Hymenolepis weldensis* Gardner & Schmidt, 1988 and *Moniliformis clarki* from the small intestines.

Falcón-Ordaz et al. (2006) described *Vexillata geomyos* from Attwater's pocket gopher, *Geomys attwateri* from the Welder Wildlife Refuge of San Patricio County, Texas.

Using molecular methods, Haukisalmi et al. (2010) documented *Hymenolepis weldensis* from *Geomys bursarius* collected from Illinois and Indiana.

Makarikov et al. (2012) described *Arostrilepis schilleri* obtained from the Camas pocket gopher, *Thomomys bulbivorus*, captured southeast of Corvallis, Oregon and originally reported as *H. horrida* by Gardner (1985).

LeBrasseur (2017) in an unpublished master's thesis reported a study focused on the endoparasites of four species of pocket gophers in the genus *Geomys* collected from eight counties in Texas. These host species included the Plains pocket gopher, *Geomys bursarius*, Attwater's pocket gopher, *G. attwateri* Merriam, 1895, Texas pocket gopher, *G. personatus* True, 1889, and the Central Texas pocket gopher *G. texensis* Merriam, 1895. In addition, she found an unidentified *Hymenolepis* Weinland, 1858 obtained from *G. attwateri*, *G. bursarius*, and *G. texensis* and another tapeworm, *Monoecocestus* was obtained from *G. bursarius*, and *G. texensis*. Finally, a nematode species, *Protospirura ascaroidea*, was found from all four species of *Geomys* mentioned above; the specimens were verified by HWML personnel (LeBrasseur 2017).

Gardner et al. (2020) described two new species of unarmed hymenolepidid tapeworms, including *Hobergia irazuensis* from the small intestine of *Heterogeomys heterodus* (Peters, 1865), collected from Potrero Cerrado, Cartago, Costa Rica, and *Hymenolepis cratogeomyos* from the small intestine of the Volcán De Toluca pocket gopher, *Cratogeomys planiceps* (Merriam, 1895) collected from Parque Nacional Nevado de Toluca, México. Also, *H. weldensis* Gardner & Schmidt, 1988 has been documented from many individuals of *Geomys lutescens* Merriam, 1890 collected in the Sandhills, on the north side of the North Platte River near Cedar Point Biological Station in western Nebraska.

The present study reports an unidentified *Monoecocestus* sp. Beddard, 1914 (probably *M. anoplocephaloides*) from the small intestine of the Yellow-faced pocket gopher, *Cratogeomys castanops* (Baird, 1852), collected by a local landowner from Black Mesa, Oklahoma in 2016 (NP2779). *Anoplocephaloides variabilis* (Douthitt, 1915) was found from the small intestine of Hall's pocket gopher, *Geomys jugossicularis* Hooper, 1940 collected from Grama grass habitat, Keith County, Nebraska in 2016 (NP2661). Also, from 2009–2016, necropsies of *Geomys lutescens* Merriam, 1890 yielded many individuals of *Litomosoides westi* Gardner & Schmidt, 1986 from their abdominal cavities with individuals of *Ransomus rodentorum* from the cecum, and from two pocket gophers *Physaloptera limbata* Leidy, 1856 was found (NP2297, NP2298). Also, during general collecting in the area of Nebraska, we found two nematode species (*R. rodentorum*, and *T. fossor* – refer to NP1524) from the cecum of the Wyoming pocket gopher, *Thomomys clusius* Coues, 1875, collected from 5 miles east of Woods Landing, Albany County, Wyoming in 2013. All specimens mentioned in this work are deposited in the HW Manter Laboratory of Parasitology Museum collection where NP refers to the field collection number.

Endoparasites of Neotropical subterranean rodents

See graphical summary in Fig. 4 and endoparasite list Table 5.

Khalil and Vogelsang (1931) described the first helminth parasite from a subterranean host from Neotropical region, *Paraspidodera americana* Khalil & Vogelsang, 1931 from the cecum of a single individual of what they called *Ctenomys magellanicus* Bennett, 1836 collected from Carrasco near Montevideo, Uruguay in 1927. The identifica-

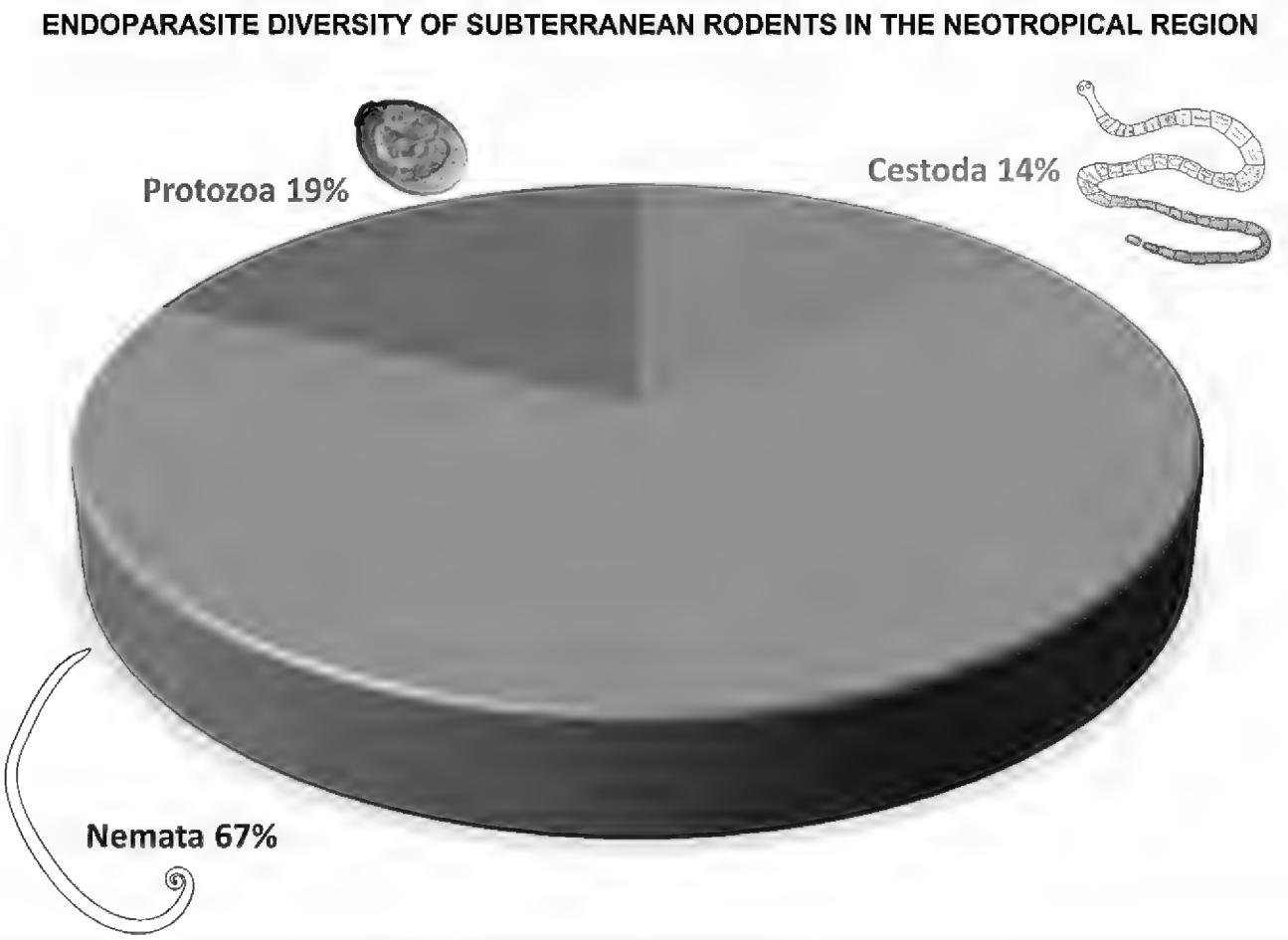

Figure 4. Percentage taxon composition of endoparasite diversity pie diagram shown by higher classification of both protozoa and helminths occurring in subterranean rodents (Family Ctenomyidae) in the southern Neotropical region. All records of parasites presented were derived from a review of the literature published from 1931 through 2021. Approximately 67% of the total endoparasite fauna of these rodents consists of Nemata, followed by Protozoa (19%), and Cestoda (14%).

tion of this mammal specimen was probably erroneous as *C. magellanicus* occurs only near the Strait of Magellan in southern Argentina). Unfortunately, no hosts or parasite specimens were deposited in any collection that we can find up to the current time.

Dollfus (1960) described *Taenia talicei* Dollfus, 1960 from the abdominal cavity of the Collared tuco-tuco, *Ctenomys torquatus* Lichtenstein, 1830, collected from Uruguay and in 1986, multistrobilate larvae of *T. talicei* were collected from several *Ctenomys opimus* at 7 km S: 4 km E. Cruce Ventilla, Oruro, Bolivia by a party from the American Museum of Natural History and the Museum of Southwestern Biology (Anderson 1997).

Olsen (1976) described *Monoecocestus torresi* obtained from the small intestine of Maule's tuco-tuco, *Ctenomys maulinus* Philippi, 1872 collected near Lonquimay, Chile. Meanwhile, Torres et al. (1976) reported *Paraspidodera uncinata* Rudolphi, 1819, and unidentified *Trichuris* are reported from Maule's tuco-tuco, *Ctenomys maulinus*, collected from Chile.

Babero and Cattan (1980) described *Graphidiodes yañezi* from the small intestine of a coruro, *Spalacopus cyanus* (Rodentia: Octodontidae), collected from near Concón, Chile.

Babero and Murua (1987) described a new species of whipworm, *Trichuris fulvi* obtained from the cecum of the Tawny tuco-tuco, *Ctenomys fulvus* Philippi, 1860, collected from San Pedro Atacama, Tarapaca province, Chile.

Lambert et al. (1988) described four new coccidian parasites in the genus *Eimeria* Schneider, 1875 recovered from the feces of the Highland tuco-tuco, *Ctenomys opimus* Wagner, 1848, trapped from several localities of the Department of Oruro, Bolivia, South America. Those species are *E. granifera* from Rancho Huancaroma, near the Rio Desaguadero, *E. montuosi*, from the north of Pomata Ayte, Rio Barros, *E. opimi*, and *E. oruroensis*, from the northeast and east of Rancho Huancaroma.

Babero and Murua (1990) described *Trichuris robusti* from the cecum and large intestine of the Tawny tuco-tuco, *Ctenomys fulvus*, collected from La Hauyca, Tarapaca province, Chile.

Gardner and Duszynski (1990), during a study on morphometric comparison of a coccidian species, *Eimeria opimi* Lambert et al., 1988, in different regions of Bolivia, the following host species were detected positive for this protozoan parasite. Those hosts include Lewis's tuco-tuco, *Ctenomys lewisi* Thomas, 1926, collected from the areas of the high-altitude region in Tarija; the Reddish tuco-tuco, *Ctenomys frater* Thomas, 1902, collected from medium latitude region of Tarija; the Conover's tuco-tuco, *Ctenomys conoveri* Osgood, 1946, collected from Chaco thorn forest area in Chuquisaca; the Bolivian tuco-tuco, *Ctenomys boliviensis* Waterhouse, 1848, and the Steinbach's tuco-tuco, *Ctenomys steinbachi* Thomas, 1907 collected from the Tropical palm/savanna region of Santa Cruz, Bolivia. In addition, the following coccidian parasites were reported from the Highland tuco-tuco, *Ctenomys opimus*. These species include *Eimeria opimi*, *E. granifera* Lambert et al., 1988, *E. oruroensis* Lambert et al., 1988, and *E. montuosi* Lambert et al., 1988 collected from the Oruro region *E. opimi* and *E. granifera* collected from the Potosi region.

Suriano and Navone (1994) described *Trichuris bursacaudata* obtained from the cecum of the Talas tuco-tuco, *Ctenomys talarum* Thomas, 1898 collected from Punta Indio, Buenos Aires, and *T. pampeana* found in the cecum of the Azara's tuco-tuco, *Ctenomys azarae* Thomas, 1903, collected from Santa Rosa, La Pampa, Argentina (Suriano and Navone 1994). However, *T. pampeana* has been redescribed from its original voucher specimens (Rossin and Malizia 2005).

Brant and Gardner (1997) described *Litomosoides andersoni* and *L. ctenomyos* from the abdominal and thoracic regions of the Highland tuco-tuco, *Ctenomys opimus*, collected from near Rancho Huancaroma, Departamento de Oruro, Bolivia.

Rossin and Malizia (2002), during a study of the relationship between helminth parasites and demographic attributes of a population, two unidentified helminth parasites were reported. Those include *Heligmostrongylus* Travassos, 1917 found in the small intestine, and *Trichuris* recovered from the cecum of the Talas tuco-tuco, *Ctenomys talarum*, collected from Necochea, Buenos Aires province, Argentina.

Rossin et al. (2004a) reported larvae of *Hydatigera* (syn. *Taenia*) *taeniaeformis* from the peritoneal cavity and liver of the Talas tuco-tuco, *Ctenomys talarum*, trapped in the

Table 5. Endoparasite species diversity from Neotropical subterranean rodents (Ctenomyidae and Octodontidae). Authorities are given for parasite and host species.

Host species	Parasite species	References
Ctenomys andersoni Gardner, et al., 2014	*Paraspidodera* Travassos, 1914	Gardner et al. 2021
Ctenomys australis Rusconi, 1934	*Pudica ctenomydis* Rossin et al., 2006	Rossin et al. 2010a
	Taenia talicei Dollfus, 1960	Rossin et al. 2010b
	Trichuris pampeana Suriano & Navone, 1994	Rossin et al. 2010a
Ctenomys azarae Thomas, 1903	*Trichuris pampeana* Suriano & Navone, 1994	Suriano and Navone 1994; Rossin and Malizia 2005a
Ctenomys boliviensis Waterhouse, 1848	*Ancylostoma ctenomyos* Drabik & Gardner, 2019	Drabik and Gardner 2019
	Paraspidodera Travassos, 1914	Gardner et al. 2021
	Eimeria opimi Lambert et al., 1988	Gardner and Duszynski 1990
Ctenomys conoveri Osgood, 1946	*Eimeria opimi* Lambert et al., 1988	Gardner and Duszynski 1990
	Paraspidodera Travassos, 1914	Gardner et al. 2021
Ctenomys erikacuellarae Gardner et al., 2014	*Paraspidodera* Travassos, 1914	Gardner et al. 2021
Ctenomys andersoni Gardner, et al., 2014	*Paraspidodera* Travassos, 1914	Gardner et al. 2021
Ctenomys australis Rusconi, 1934	*Pudica ctenomydis* Rossin et al., 2006	Rossin et al. 2010a
	Taenia talicei Dollfus, 1960	Rossin et al. 2010b
	Trichuris pampeana Suriano & Navone, 1994	Rossin et al. 2010a
Ctenomys azarae Thomas, 1903	*Trichuris pampeana* Suriano & Navone, 1994	Suriano and Navone 1994; Rossin and Malizia 2005a
Ctenomys boliviensis Waterhouse, 1848	*Ancylostoma ctenomyos* Drabik & Gardner, 2019	Drabik and Gardner 2019
	Paraspidodera Travassos, 1914	Gardner et al. 2021
	Eimeria opimi Lambert et al., 1988	Gardner and Duszynski 1990
Ctenomys conoveri Osgood, 1946	*Eimeria opimi* Lambert et al., 1988	Gardner and Duszynski 1990
	Paraspidodera Travassos, 1914	Gardner et al. 2021
Ctenomys erikacuellarae Gardner et al., 2014	*Paraspidodera* Travassos, 1914	Gardner et al. 2021
	Raillietina Fuhrman, 1920	Gardner et al. 2021
Ctenomys frater Thomas, 1902	*Eimeria opimi* Lambert et al., 1988	Gardner and Duszynski 1990
	Paraspidodera Travassos, 1914	Gardner et al. 2021
Ctenomys fulvus Philippi, 1860	*Trichuris fulvi* Babero & Murua, 1987	Babero and Murua 1987
	Trichuris robusti Babero & Murua, 1990	Babero and Murua 1990
Ctenomys lewisi Thomas, 1926	*Eimeria opimi* Lambert et al., 1988	Gardner and Duszynski 1990
	Paraspidodera Travassos, 1914	Gardner et al. 2021
Ctenomys leucodon Waterhouse, 1848	*Pudica pujoli* Durette-Casset & Tcheprakoff, 1990	Gardner et al. 2021
Ctenomys magellanicus Bennett, 1836	*Paraspidodera americana* Khalil & Vogelsang, 1931	Khalil and Vogelsang 1931
Ctenomys maulinus Philippi, 1872	*Monoecocestus torresi* Olsen, 1976	Olsen 1976
	Paraspidodera uncinata Rudolphi, 1819	Torres et al. 1976
	Trichuris Roederer, 1761	Torres et al. 1976
Ctenomys nattereri Wagner, 1848	*Paraspidodera* Travassos, 1914	Gardner et al. 2021
	Trichuris Roederer, 1761	Gardner et al. 2021
Ctenomys opimus Wagner, 1848	*Eimeria granifera* Lambert et al., 1988	Lambert et al. 1988; Gardner and Duszynski 1990
	Eimeria montuosi Lambert et al., 1988	Lambert et al. 1988; Gardner and Duszynski 1990
	Eimeria opimi Lambert et al., 1988	Lambert et al. 1988; Gardner and Duszynski 1990
	Eimeria oruroensis Lambert et al., 1988	Lambert et al. 1988; Gardner and Duszynski 1990
	Litomosoides andersoni Brant & Gardner, 1997	Brant and Gardner 1997
	Litomosoides ctenomyos Brant & Gardner, 1997	Brant and Gardner 1997
	Mathevotaenia Akhumyan, 1946	Gardner et al. 2021, 2023
Ctenomys pearsoni Lessa & Langguth, 1983	*Strongyloides myopotami* Artigas & Pacheco, 1933	Rossin et al. 2009
Ctenomys steinbachi Thomas, 1907	*Ancylostoma ctenomyos* Drabik & Gardner, 2019	Drabik and Gardner 2019
	Eimeria opimi Lambert et al., 1988	Gardner and Duszynski 1990
	Paraspidodera Travassos, 1914	Gardner et al. 2021
Ctenomys talarum Thomas, 1898	*Graphidiodes subterraneus* Rossin et al., 2005	Rossin et al. 2005b; Rossin et al. 2010b
	Heligmostrongylus Travassos, 1917	Rossin and Malizia 2002
	Paraspidodera uncinata Rudolphi, 1819	Rossin et al. 2004b; Rossin et al. 2010b
	Pudica ctenomydis Rossin et al., 2006	Rossin et al. 2006a; Rossin et al. 2010b
	Strongyloides myopotami Artigas & Pacheco, 1933	Rossin et al. 2010b; Rossin et al. 2009

Host species	Parasite species	References
Ctenomys talarum Thomas, 1898	*Hydatigera* (syn. *Taenia*) *taeniaeformis* Batsch, 1786	Rossin et al. 2004a
	Taenia talicei Dollfus, 1960	Rossin et al. 2010a; Rossin et al. 2010b
	Trichostrongylus duretteae Rossin et al., 2006	Rossin et al. 2006b; Rossin et al. 2010a
	Trichuris Roederer, 1761	Rossin and Malizia 2002; Rossin and Malizia 2005a
	Trichuris bursacaudata Suriano & Navone, 1994	Suriano and Navone 1994
	Trichuris pampeana Suriano & Navone, 1994	Rossin et al. 2010a; Rossin and Malizia 2005a
Ctenomys torquatus Lichtenstein, 1830	*Taenia talicei* Dollfus, 1960	Dollfus 1960
Spalacopus cyanus (Molina, 1782)	*Graphidioides yañezi* Babero & Cattan, 1980	Babero and Cattan 1980

urban areas of Mar de Cobo, Buenos Aires province, Argentina. These authors experimentally infected dogs with this species of tapeworm from the tucos and recovered adult cestodes.

Rossin et al. (2004b) redescribed *Paraspidodera uncinata* (Rudolphi, 1819) from a large number of specimens obtained from the cecum and large intestine of the Talas tuco-tuco, *Ctenomys talarum*, collected from Mar de Cobo, Buenos Aires province, Argentina.

Rossin and Malizia (2005a) redescribed *Trichuris pampeana* Suriano & Navone, 1994 found in the cecum of the Azara's tuco-tuco, *Ctenomys azarae*, collected from Santa Rosa, La Pampa province, and reported new voucher material, the Talas tuco-tuco, *C. talarum* Thomas, 1898, collected at the Necochea, coastal dunes of Buenos Aires province. Also, an unidentified *Trichuris* found in *C. talarum* collected from Buenos Aires province, Argentina was reported. Simultaneously, Rossin et al. (2005b) described *Graphidiodes subterraneus* from the stomach of the Talas tuco-tuco, *Ctenomys talarum*, collected from Mar de Cobo, Partido de Mar Chiquita, Mar del Plata, Argentina.

Continuing work on tucos, Rossin et al. (2006a) described *Pudica ctenomydis* from the small intestine of the Talas tuco-tuco, *Ctenomys talarum*, collected from Mar de Cobo, Partido de Mar Chiquita, Argentina. In the same year, Rossin et al. (2006b) described *Trichostrongylus duretteae* obtained from the small intestine of the Talas tuco-tuco, *Ctenomys talarum*, collected from Mar de Cobo, Buenos Aires province, Argentina.

Rossin et al. (2009) reported *Strongyloides myopotami* Artigas & Pacheco, 1933 found in the small intestines of the Talas tuco-tuco, *Ctenomys talarum*, collected from Mar de Cobo, Buenos Aires province, Argentina, and from Pearson's tuco-tuco, *Ctenomys pearsoni* Lessa & Langguth, 1983, collected from Penino, Departamento de San José, Uruguay.

During an ecological study of helminth parasite infection parameters in two species of South American subterranean rodents of the genus *Ctenomys*, Rossin et al. (2010a) documented seven species of Endoparasites from two collection localities, species of hosts studied included the Southern tuco-tuco, *C. australis* Rusconi, 1934, from Necochea, Buenos Aires Province, and Talas tuco-tuco, *C. talarum* Thomas, 1898, from Mar de Cobo, Buenos Aires province, Argentina. Both species of tuco-tuco's harbored *Trichuris pampeana* in the cecum, *Pudica ctenomydis* Rossin et al., 2006 in the small intestine, and larvae of *Taenia talicei* in the abdominal cavity. Moreover, *C. talarum*

had four additional species of helminths, including *Graphidiodes subterraneus* Rossin et al., 2005 in the stomach, *Paraspidodera uncinata* in the large intestine, and *Strongyloides myopotami* and *Trichostrongylus duretteae* Rossin et al., 2006 in the small intestine.

Rossin et al. (2010b) redescribed the metacestode form of *Taenia talicei* obtained from the peritoneal cavity of two tuco-tuco species including the Southern tuco-tuco, *Ctenomys australis* Rusconi, 1934, and the Talas tuco-tuco, *Ctenomys talarum*, from Necochea, Paraje Las Grutas, Buenos Aires Province in Argentina.

From Bolivia, Drabik and Gardner (2019) described *Ancylostoma ctenomyos* Drabik & Gardner, 2019 from the small intestine of the Bolivian tuco-tuco, *Ctenomys boliviensis* collected from two localities in the Department of Santa Cruz, 3.5 km west of Estación el Pailón and 2 km SSE of Santa Rosa de la Roca, and from Steinbach's tuco-tuco, *Ctenomys steinbachi* Thomas, 1907 collected from 2 km S. of Caranda by road in the Department of Santa Cruz.

Gardner et al. (2021) mentioned discovery of a new species of *Mathevotaenia* from the Highland tuco-tuco, *Ctenomys opimus*, collected in 1986 from Huancaroma, Department of Oruro, Bolivia (Gardner et al. 2023). Also from Bolivia, Gardner et al. (2021) also reported *Paraspidodera* nematodes including individuals from the cecae of Anderson's tuco-tuco, *Ctenomys andersoni* Gardner et al., 2014, the Bolivian tuco-tuco or Cajuchi, *Ctenomys boliviensis* Waterhouse, 1848, Conover's tuco-tuco, *Ctenomys conoveri* Osgood, 1946, Erica's tuco-tuco, *Ctenomys erikacuellarae* Gardner et al., 2014, the little Andean forest tuco-tuco, *Ctenomys frater* Thomas, 1902, Lessa's tuco-tuco, *Ctenomys lessai* Gardner et al., 2014, Lewis's tuco-tuco, *Ctenomys lewisi*, Steinbach's tuco-tuco, *Ctenomys steinbachi*, and Natterer's tuco-tuco, *Ctenomys nattereri* Wagner, 1848. In addition, an undescribed species of *Raillietina* was found in the small intestine of *C. erikacuellarae* collected on the experiment station grounds near Monteagudo, Bolivia and *Pudica* sp. Travassos & Darriba, 1929 was also reported from the White-toothed tuco-tuco, *Ctenomys leucodon* Waterhouse, 1848.

The present study reports that during a biodiversity survey in Bolivia in 1986, *Pudica pujoli* Durette-Desset & Tcheprakoff, 1990 was found in a single specimen of the White-toothed tuco-tuco, *Ctenomys leucodon* Waterhouse, 1848, collected from near San Andreas de Machaca, Bolivia.

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